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A New Genus for the Extinct Late Pleistocene Owl *Strix brea* Howard (Aves: Strigiformes) from Rancho La Brea, California

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ABSTRACT. We review all of the fossil specimens from the upper Pleistocene Rancho La Brea asphalt deposits previously referred to the extinct owl *Strix brea*, and all newly identified specimens referable to that species. This review and emended description of *Strix brea* have provided a clearer picture of this species, and we find that it is more appropriately placed in a new genus, *Oraristrix*, whose affinities remain unclear. We provide a variety of morphometric data and more detailed osteological descriptions of this extinct owl based on 138 specimens from the Rancho La Brea collections in the George C. Page Museum that represent a minimum of 23 individuals. An additional nine specimens of this extinct species were confirmed in collections from the upper Pleistocene asphalt deposits of Carpinteria, California. *Oraristrix brea* is interpreted as being more terrestrial in habits than forest owls because, compared to available species of the genera *Bubo* and *Strix*, it had longer legs relative to its wingspan.

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A large, extinct owl from the upper Pleistocene asphalt deposits of Rancho La Brea, California was described as *Strix brea* Howard, 1933. In addition to the holotypic tarsometatarsus, several other elements of the skeleton were briefly described and referred to this species by Howard (1933). However, since its original description, with the exception of being included in faunal lists (e.g., Howard, 1962), this species, which is known as the Brea Owl, has not been revisited. Herein we reevaluate the characters Howard (1933) used to distinguish the species, describe additional characters, illustrate bones not previously illustrated, and add to the list of elements and specimens referable to this extinct species. We offer suggestions as to the size and life habits of the Brea Owl based on its osteology and limb bone proportions. *Strix brea* is found to be a valid species, but one best placed in a new genus.

This study is part of an overall review of all of the fossil owls in the collections from Rancho La Brea maintained at the George C. Page Museum by the Natural History Museum of Los Angeles County (LACM). At least nine species of owls are represented in the collections by a total of over 7500 specimens. In the course of this review we found that the post-cranial elements of the genera of owls could be fairly easily distinguished by osteological characters, at least for the

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several genera represented in the Rancho La Brea collection. This finding is contrary to that of Olson & James (1991), who, citing an unpublished work by Ford (1967), suggested that post-cranial differences between the various subgroups and genera of owls are very slight or non-existent.

Materials and methods

The fossil specimens were compared in detail with specimens of modern *Bubo virginianus* (20+) and all of the numerous fossil specimens of *B. virginianus* from Rancho La Brea, *B. bubo* (4), *B. africanus* (1), *Strix occidentalis* (8), *S. varia* (7), *S. nebulosa* (9), and *S. aluco* (3). The numbers reflect the largest sample sizes of each species available for comparison. Points on scatter diagrams are often less numerous because of incomplete modern comparative specimens. The genera *Ketupa* and *Nyctea* are considered by some (Amadon & Bull, 1988; Wink & Heidrich, 1999; Wink *et al*., 2008) as properly being included within *Bubo*, so these genera were included in our study. *Nyctea*, for the most part, agrees with *Bubo* as far as the osteological characters useful for distinguishing the Brea Owl from *Bubo* and *Strix* are concerned. *Ketupa* [*K. ketupa* (1), *K. zeylonensis* (3)], on the other hand, varies considerably from *Bubo* osteologically, and we find it to be easily distinguished from both *Bubo* and the Brea Owl. In our opinion, based on its osteological features, we agree with Sibley & Monroe (1990) that *Ketupa* is a valid genus separate from *Bubo*. However, we were unable to compare the species of *Ketupa* with those Asian species of *Bubo* that Wink & Heidrich (1999) and Wink *et al*. (2008) suggested were closest to *Ketupa* based on molecular studies.

Similarly, the genus *Ciccaba* is considered by some as properly being included within *Strix* (e.g., Sibley & Monroe, 1990; Wink & Heidrich, 1999; Wink *et al*., 2008), and we found that two species referred to *Ciccaba* [*C. virgata* (1) and *C. nigrolineata* (1)] agree with *Strix* as far as most of the osteological characters we detail below are concerned. Based on the osteology of available specimens, we accept that *Nyctea* belongs within *Bubo* and *Ciccaba* within *Strix*. Comparisons were also made with the genera *Tyto, Otus, Megascops, Lophostrix, Pulsatrix, Surnia, Glaucidium, Athene, Aegolius, Micrathene, Ninox*, and *Asio*. Each of these genera can be readily distinguished from *Bubo, Strix*, and the Brea Owl using osteological characters. In molecular studies, *Strix* and *Bubo* appear as closely related taxa (Wink & Heidrich, 1999; Wink *et al*., 2008), which is reflected in the many osteological characters they share that differ significantly from those of the other genera examined. Therefore, because this study was not intended as a comparative osteological review of all genera of owls we limit our detailed comparisons to species of *Bubo* and *Strix*, the genera that most closely resemble the Brea Owl osteologically.

Measurements were taken using digital calipers accurate to 0.01 mm, and all data were captured directly to computer. The measurements were stored, and the basic statistics, including minimum, maximum, arithmetic mean, and standard deviations, were computed in Microsoft Excel. For illustrations as to how the measurements were taken, see Appendix 2. All bones were checked for ratios useful for differentiating the species, and scatter diagrams of the ratios were prepared using Microsoft Excel and Corel Photo-Paint. Osteological terminology is primarily from Baumel & Witmer (1993). Abbreviations used: *Cond*. = condylus; *Fac. artic*. = facies articularis; *Lig. coll*. = ligamentum collaterale; *Proc*. = processus; *Tub*. = tuberulum

Figure 1. Holotypic tarsometatarsus of *Oraristrix brea* (LACM RLB E9379) in (*A*) anterior, (*B*) lateral, (*C*) posterior, (*D*) medial, (*E*) proximal, and (*F*) distal views. Lateral view (*G*) of distal tarsometatarsus of *O. brea* (LACM RLB K9623) illustrates the straight posterior edge of the lateral condyle of Trochlea III. Scale bar = 20 mm.

Systematics

Order Strigiformes

Family Strigidae

Oraristrix new genus

Type and only included species. *Strix brea* Howard, 1933.

Diagnosis. The tarsometatarsus of *Oraristrix* (Fig. 1) is diagnosed by having (1) Crista medialis hypotarsi with posterior surface long and relatively narrow (posterior surface broad, narrow, or egg-shaped, but moderately long to short in *Strix*; posterior surface either egg-shaped or broad, moderately long to short in *Bubo*); (2) Crista medialis hypotarsi with medial edge of posterior surface concave, in posterior view (posterior surface with variable medial edge in *Strix*; posterior surface rarely with slightly concave medial edge in *Bubo*); (3) Crista medialis hypotarsi extending posteriad and laterad such that posterior lateral edge of hypotarsus lies farther laterally than anterior base (extends less laterad in *Strix*; extends posteriad closer to perpendicular to transverse plane of bone in *Bubo*); (4) Crista medialis hypotarsi with internal side deeply concave (internal side moderately to deeply concave in *Strix* and moderately concave in *Bubo*); (5) Crista medialis hypotarsi bordered medially by prominent angular ridge (a moderate to strongly angular ridge present in *Strix* and only a weak, rounded ridge present in *Bubo*); (6) Cotyla lateralis with posterolateral process, in lateral view, joining posterolateral edge of shaft rather abruptly (process joins posterolateral edge of shaft abruptly to gradually in *Strix*; process joins posterolateral edge of shaft gradually in *Bubo*); (7) Trochlea metatarsi II, in medial view, with "wing" directed posteriad, or plantarad, and with only a slight trend distad (more rounded, in medial view, with posterodistal corner with significant turn distad in *Strix* and *Bubo*); (8) Trochlea metatarsi III, in distal view, with external rim bulging laterad sufficiently to hide distal foramen (similar, but not as extreme, in *Strix*; does not bulge laterad sufficiently to hide distal foramen in *Bubo*); (9) Trochlea metatarsi III with lateral rim straight posteriorly, in lateral view (similar in *Strix*; lateral rim anteroposteriorly rounded and projecting much farther posteriad than medial rim, in lateral view, in *Bubo*); (10) Trochlea metatarsi IV extends farther distad relative to Trochlea metatarsi III than that of *Strix* and much farther distad relative to Trochlea metatarsi III of *Bubo*.

Etymology. *Oraristrix*, from *orarius*, Latin, of the coast, and *strix*, Latin, owl. In reference to the species' known late Pleistocene distribution in coastal southwestern California.

Oraristrix brea (Howard, 1933), new combination

Strix brea Howard, 1933, (March 17), *Condor* 35(2), p. 66, fig. 15 [sic].

Figs 1, 4–6, 8

Types. HOLOTYPE, complete left tarsometatarsus, LACM RLB E9379. PARATYPES: Rancho La Brea: 8 complete right and 9 complete left tarsometatarsi; 1 proximal right and 1 distal left tarsometatarsus.

Referred material. Rancho La Brea: Rostrae maxillare, 2; mandible, 1 anterior with symphysis; sternae, 3; scapulae, 5 right, 9 left; coracoids, 5 complete and 1 scapular end right, 4 complete and 2 scapular ends left; clavicula, 1 right dorsal end; humeri, 3 complete right and 2 complete left, 1 proximal right and 2 proximal left, 1 distal right and 2 distal left; ulnae, 1 complete right, 3 proximal right and 2 proximal left, 2 distal right and 2 distal left; radii, 5 proximal left, 2 distal right and 2 distal left; carpometacarpi, 7 complete right and 4 complete left, 2 distal right; femora, 2 complete right and 3 complete left, 2 proximal left, and 5 distal right and 5 distal left; tibiotarsi, 2 complete right and 3 complete left, 1 proximal right and 5 proximal left, 9 distal right and 3 distal left; fibulae, 3 proximal left; pelves, 2. For catalogue numbers, see Appendix 1.

Carpinteria. Locality LACM(CIT) 139: Rostrum maxillare, 1; coracoids, 1 right and 1 left; humeri, 1 complete left and 1 proximal left; carpometacarpus, 1 incomplete left; tarsometatarsus, 1 complete left. Collections of Santa Barbara Museum of Natural History: Coracoid, sternal end, left; tibiotarsus, distal, right.

Emended diagnosis. As for genus.

Type locality and horizon. Asphalt deposits of Rancho La Brea, at a depth of 3.7–4.9 m (12–16 feet) in Pit 16, Los Angeles, California.

Age. Late Pleistocene.

Description. *Oraristrix brea* was approximately the same size overall as modern *Bubo virginianus* and *Strix nebulosa*, but it was far larger than both *S. varia* and *S. occidentalis*, as noted by Howard (1933). In general, the bones of *O. brea* are more slender, or more lightly built, than those of both *B. virginianus* and *S. nebulosa*, although some elements are more robust in some measurements. *Oraristrix brea* also differs in its limb proportions from those species. Thus, in addition to the diagnostic osteological characters, differences between *Oraristrix, Strix*, and *Bubo* are apparent in both intra- and inter-element and intermembral proportions (see, e.g., Figs 2, 3). For measurements of all elements, see Table 1.

Tarsometatarsus (Figs 1A–G, 2, 3). This bone was discussed in greater detail than any other by Howard (1933), who described five morphological characters and a number of ratios differentiating the extinct species from *Strix occidentalis, S. varia*, and *Bubo virginianus*. Our characters 1, 2, 3, and 9 above are four of these characters that we found to hold up well with our larger comparative series of modern species. However, we found that Howard's (1933:66) distinguishing character 2 ("distal margin of this surface [i.e., posterior, or plantar, surface of internal calcaneal ridge] (as seen in lateral view) sharply defined from portion of calcaneal ridge immediately distal to it, even overhanging") did not consistently distinguish *Oraristrix brea*.

Rostrum maxillare (Fig. 4A–C). Characterized by having (1) Os nasale with posterior edge sloping steeply anteriad, in lateral view [sloping significantly less steeply in *Bubo* (except in *Nyctea* where slope is similar to that of *Oraristrix*) and *Strix*]; (2) Fossae nasales with long axis at steeper angle to Crista tomialis than in either *Bubo* or *Strix*; (3) Fossae nasales with internal floor deeply excavated, nearly parallel to tomial margin (floor of nares similar in *Bubo*; much less excavated in *Strix*); (4) Crista tomialis extends posteriad ventral to, and separated from, Proc. jugalis for a significant distance, ending as pointed projection (similar to shorter in *Bubo*; extends posteriad under Proc. jugalis only slightly, if any, in *Strix*).

Howard's (1933) only criterion for distinguishing the Rostra maxillare of *Oraristrix* from the many partial *Bubo* specimens in the collection (i.e., turbinates more widely

Table 1. Measurements (mm) of skeletal elements of the late Pleistocene *Oraristrix brea* compared with extant species and fossil *Bubo virginianus* from Rancho La Brea (see Figs 10 and 11 for illustrations of measurements). Measurements given in the order: (number of specimens) arithmetic mean ± standard deviation [observed range].

Measurements	***Bubo bubo***	***Bubo virginianus***	***Bubo virginianus* (fossil)**	***Oraristrix brea* (fossil)**
Premaxilla				
Anterior height (A)	(4) 12.61±0.69 [11.7–13.3]	(20) 11.42±0.63 [10.41–12.53]	(0)	(3) 12.37±0.37 [12.14–12.79]
Anterior width (B)	(4) 12.50±1.25 [11.07–14.05]	(20) 9.46±0.62 [8.15–10.54]	(0)	(3) 10.56±1.29 [9.19–11.76]
Posterior height (C)	(4) 22.53±0.78 [21.64–23.48]	(20) 20.33±1.09 [18.26–21.91]	(2) [20.29–20.44]	(2) [21.61–22.2]
Tomial length (D)	(4) 32.34±2.13 [29.45–34.45]	(20) 28.05±1.28 [26.08–30.79]	(2) [28.41–31.45]	(3) 30.57±0.89 [29.66–31.44]
Tomial width (E)	(4) 28.65±2.01 [26.57–31.05]	(20) 24.09±1.57 [21.76–28.08]	(1) 24.01	(3) 25.22±2.6 [23.4–28.19]
Sternum				
Total length (A)	(4) 81.9±6.08 [73.27–86.77]	(16) 59.46±4.32 [53.26–72.5]	(6) 66.99±1.37 [64.87–68.48]	(1) 59.23
Ventral width (B)	(4) 38.79±2.59 [36.69–42.42]	(17) 29.72±2.31 [27.29–35.8]	(6) 34.25±1.46 [32.75–36.75]	(3) 29.33±3.55 [26.46–33.3]
Coracoid				
Medial length (A)	(3) 63.01±0.35 [62.6–63.22]	(18) 49.03±3.01 [45.23–55.48]	(28) 53.27±1.66 [50.05–57.05]	(10) 47.68±1.65 [44.56–49.32]
Depth of acrocoracoid (B)	(4) 11.75±0.48 [11.06–12.15]	(18) 9.00±0.68 [7.88–10.59]	(28) 9.68±0.46 [8.66–10.42]	(13) 8.85±0.46 [7.95–9.29]
Width of acrocoracoid (C)	(4) 9.87±0.45 [9.32–10.38]	(18) 7.33±0.61 [6.46–8.76]	(28) 8.07±0.46 [7.05–8.96]	(12) 6.48±0.41 [5.48–7]
Width of shaft at procoracoid (D)	(4) 14.53±0.57 [14.17–15.38]	(16) 10.25±0.76 [9.41–12.04]	(28) 11.33±0.52 [10.41–12.46]	(8) 9.31±0.57 [8.22–10.13]
Scapula				
Articular length (A)	(4) 18.71±1.04 [17.59–19.68]	(19) 14.99±1.11 [13.59–18.18]	(43) 16.48±0.84 [14.53–18.09]	(11) 14.06±0.6 [12.75–14.84]
Length of Fac. artic. humeralis (B)	(4) 13.05±0.62 [12.47–13.64]	(19) 9.38±0.74 [8.45–11.27]	(43) 10.5±0.58 [9.36–11.83]	(11) 8.89±0.51 [8.13–9.49]
Width of Fac. artic. humeralis (C)	(4) 8.49±0.47 [8.08–9.16]	(19) 6.42±0.51 [5.64–7.9]	(43) 7.2±0.45 [6.28–8.29]	(11) 6.36±0.4 [5.65–6.81]
Humerus				
Total length (A)	(4) 165.04±10.4 [150.74–174.8]	(18) 124.34±6.15 [113.8–136.82]	(6) 133.59±5.61 [125.37–138.67]	(4) 117.07±3.76 [112.58–121.27]
Proximal width (B)	(4) 29.59±1.9 [26.94–31.14]	(18) 21.09±1.42 [19.05–24.87]	(6) 22.67±1.28 [20.5–23.8]	(5) 20.55±0.68 [19.66–21.24]
Distal width (C)	(4) 27.88±1.56 [25.6–29.08]	(18) 20.32±1.37 [18.49–24.06]	(6) 21.83±1.42 [19.62–23.05]	(6) 19.44±0.57 [18.35–19.91]
Radius				
Total Length (A)	(4) 184.2±11.91 [167–192.3]	(20) 137.21±5.82 [126.62–149.11]	(3) 146.75±7.02 [138.84–152.25]	(0)
Maximum proximal width (B)	(4) 9.69±0.42 [9.16–10.19]	(20) 7.36±0.5 [6.72–9]	(3) 7.97±0.46 [7.46–8.36]	(4) 6.93±0.82 [5.73–7.57]
Minimum proximal width (C)	(4) 6.3±0.57 [5.46–6.69]	(20) 4.55±0.35 [4.02–5.58]	(3) 5.07±0.41 [4.61–5.41]	(5) 4.07±0.11 [3.9–4.22]
Distal width (D)	(4) 13.24±1.32 [11.66–14.88]	(20) 9.78±0.6 [8.77–11.84]	(3) 11±0.58 [10.38–11.53]	(3) 9.64±0.35 [9.37–10.04]
Ulna				
Total Length (A)	(4) 191.1±12.51 [173.1–199.8]	(19) 143.03±6.31 [132.03–157.8]	(6) 154.41±5.48 [147.09–160.5]	(1) 138.25
Proximal width (B)	(4) 17.75±1.08 [16.16–18.57]	(19) 12.95±0.99 [11.57–15.82]	(6) 14.37±0.82 [12.81–15.08]	(1) 13.05
Proximal depth (C)	(4) 14.73±1 [13.28–15.58]	(19) 10.46±0.78 [9.41–12.32]	(6) 11.19±0.54 [10.34–12.05]	(1) 10.42
Width of Condylus dorsalis (D)	(4) 12.3±1.23 [10.69–13.49]	(19) 10.05±0.64 [8.62–11.05]	(6) 11.44±0.38 [11.1–11.94]	(1) 7.67
Carpometacarpus				
Total length (A)	(4) 87.28±5.1 [80.61–92.98]	(18) 64.32±3.13 [57.99–70.26]	(34) 69.14±2.83 [63.45–75.1]	(7) 59.71±1.63 [57.7–62.62]
Proximal width (B)	(4) 18.79±1.06 [17.65–19.98]	(18) 13.74±0.88 [12.39–15.99]	(34) 14.87±0.71 [13.13–16.21]	(7) 13.27±0.38 [12.76–13.78]
Proximal depth (C)	(4) 9.32±0.61 [8.74–9.92]	(18) 7.1±0.47 [6.39–8.4]	(34) 7.73±0.39 [6.76–8.38]	(7) 7.3±0.22 [6.92–7.52]
Depth of mid-shaft (D)	(4) 6.55±0.39 [5.97–6.83]	(18) 4.72±0.37 [3.89–5.39]	(34) 5.09±0.3 [4.35–5.59]	(8) 4.89±0.17 [4.64–5.21]
Distal width (E)	(4) 13.45±0.82 [12.38–14.32]	(18) 10.68±0.73 [9.49–12.46]	(34) 11.82±0.58 [10.62–12.87]	(9) 10.95±0.35 [10.48–11.53]
Pelvis				
Neural arch height (A)	(4) 16.34±1.35 [14.47–17.53]	(19) 11±0.9 [9.86–12.72]	(7) 13.11±0.65 [12.04–14.21]	(2) [10.22–10.39]
Centre height through vertebra (B)	(4) 26.95±2.03 [24.73–29.63]	(19) 18.71±1.2 [17.02–20.68]	(7) 21.47±1.38 [19.19–22.86]	(2) [18.21–18.5]
Width through prezygapop (C)	(4) 13.2±0.88 [12.19–14.33]	(19) 10.06±0.59 [9.12–11.21]	(7) 10.77±0.63 [9.43–11.3]	(2) [10.53–10.76]
Width through antitrochanter (D)	(4) 47.58±1.51 [45.67–49.36]	(19) 37.09±1.9 [34.67–41.86]	(7) 42.48±1.97 [39.13–45.24]	(2) [38.4–38.4]
Width through 1st transverse process (E)	(4) 26.01±1.7 [24.93–28.55]	(19) 20.42±0.92 [18.59–22.02]	(7) 22.48±1.35 [19.5–23.41]	(2) [20.63–22.09]

cont. …

Femur				
Medial length (A)	(4) 94.62±4.25 [89.85–99.89]	(18) 73.97±3.55 [68.85–82.66]	(41) 80.13±2.72 [73.82–85.12]	(5) 75.52±1.31 [73.25–76.6]
Proximal width (B)	(4) 20.53±1.01 [19.45–21.48]	(18) 15±1 [13.32–17.29]	(41) 16.91±0.76 [15.09–18.48]	(6) 14.97±0.34 [14.51–15.4]
Width at mid-shaft (C)	(4) 9.01±0.59 [8.13–9.36]	(18) 6.64±0.48 [5.82–7.74]	(41) 7.42±0.45 [6.45–8.27]	(8) 6.75±0.24 [6.47–7.13]
Depth at mid-shaft (D)	(4) 8.55±0.5 [7.84–8.99]	(18) 6.23±0.52 [5.52–7.52]	(41) 6.94±0.43 [6.09–7.94]	(8) 6.18±0.23 [5.82–6.41]
Distal width (E)	(4) 20.1±1.61 [17.92–21.63]	(18) 15.18±1.16 [13.08–18.15]	(41) 17.1±0.94 [15.23–19.11]	(10) 15.05±0.96 [12.81–16.07]
Distal depth (F)	(4) 17.49±1.79 [15.57–19.86]	(18) 12.47±0.88 [11.23–14.71]	(41) 13.68±0.92 [11.64–15.57]	(9) 12.34±0.53 [11.51–13.02]
Tibiotarsus				
Total length (A)	(4) 146.01±8.43 [134.15–153.48]	(18) 118.57±4.1 [111.78–125.95]	(18) 125.37±5.01 [115.18–133.72]	(5) 117.89±2.91 [112.85–119.92]
Proximal width (B)	(4) 17.78±1.49 [15.71–19.06]	(18) 13.36±0.91 [11.64–15.75]	(18) 14.77±0.79 [13.58–16.04]	(7) 13.3±0.45 [12.58–13.84]
Proximal depth (C)	(4) 19.95±2.5 [17.65–22.75]	(18) 15.01±1.16 [13.04–18.13]	(18) 16.59±1.01 [15.07–18.32]	(6) 15.19±0.5 [14.24–15.52]
Width at mid-shaft (D)	(4) 8.36±0.16 [8.16–8.54]	(18) 6.41±0.41 [5.69–7.35]	(18) 7.27±0.35 [6.61–7.93]	(12) 6.39±0.39 [5.76–6.89]
Distal width (E)	(4) 19.13±1.32 [17.84–20.98]	(18) 14.48±1.17 [12.48–17.36]	(18) 16.16±0.89 [14.6–17.74]	(10) 13.15±0.96 [11.62–14.21]
Cond. lateralis depth (F)	(4) 14.99±1.08 [13.48–15.95]	(18) 11.32±0.8 [9.93–13.32]	(17) 12.25±0.64 [11.45–13.32]	(8) 10.63±0.77 [9.44–11.44]
Cond. medialis depth (G)	(4) 15.95±1.03 [14.4–16.53]	(18) 11.8±0.77 [10.39–13.67]	(18) 12.97±0.71 [11.87–14.1]	(10) 10.82±0.62 [9.72–11.47]
Tarsometatarsus				
Total length (A)	(4) 78.69±3.35 [74.37–81.57]	(20) 61.17±1.88 [57.91–65.43]	(68) 65.3±2.15 [60.43–69.99]	(15) 65.71±1.47 [62.62–68]
Proximal width (B)	(0)	(20) 13.94±1.08 [12.23–16.72]	(68) 15.62±0.89 [13.51–17.4]	(17) 13.44±0.78 [12.39–14.86]
Length of hypotarsus (C)	(4) 10.82±0.68 [10.17–11.42]	(20) 6.84±0.63 [5.62–8.4]	(68) 7.86±0.71 [6.49–9.17]	(16) 8.45±0.6 [7.2–9.13]
Width of hypotarsus (D)	(4) 4.67±0.2 [4.41–4.87]	(20) 3.35±0.3 [2.89–4]	(68) 3.79±0.46 [2.92–4.99]	(14) 2.94±0.46 [2.08–3.63]
Minimum shaft width (E)	(4) 9.45±0.56 [8.78–10.1]	(20) 7.74±0.81 [6.47–9.64]	(68) 8.93±0.69 [7.24–9.93]	(16) 7.14±0.44 [6.33–7.95]
Distal width (F)	(4) 21.66±1.35 [20.00–23.24]	(20) 16.67±1.1 [14.87–19.36]	(68) 18.36±0.99 [16.26–20.12]	(14) 15.83±0.85 [14.48–17.16]

Measurements	*Strix occidentalis*	*Strix varia*	*Strix aluco*	*Strix nebulosa*
Premaxilla				
Anterior height (A)	(7) 9.44±0.44 [8.73–10]	(8) 9.77±0.42 [9.21–10.61]	(8) 7.52±0.44 [6.95–8.34]	(4) 9.98±0.6 [9.47–10.79]
Anterior width (B)	(7) 8.33±0.46 [7.39–8.77]	(8) 8.64±0.71 [7.98–9.97]	(8) 6.04±0.39 [5.45–6.66]	(4) 8.51±0.26 [8.12–8.7]
Posterior height (C)	(8) 16.4±0.43 [15.69–16.93]	(8) 16.67±1.01 [15.26–17.79]	(8) 13.81±0.47 [13.2–14.46]	(4) 19.11±1.52 [16.92–20.34]
Tomial length (D)	(8) 21.51±0.47 [20.85–22.33]	(8) 23.83±1.22 [21.38–25.2]	(8) 19.91±0.59 [18.77–20.5]	(4) 26.78±1.18 [25.7–28.05]
Tomial width (E)	(8) 17.78±0.5 [16.84–18.26]	(8) 19.31±1.09 [18.38–21.4]	(8) 17.41±0.53 [16.48–17.96]	(4) 23.22±1.53 [21.39–25.06]
Sternum				
Total length (A)	(8) 46.91±1.66 [44.2–49.34]	(7) 51.08±2.45 [47.08–54.4]	(8) 41.93±1.81 [39.21–44.54]	(4) 62.06±3.42 [59.12–66.42]
Ventral width (B)	(8) 24.76±0.89 [23.44–25.87]	(7) 25.39±1.71 [22.94–28.24]	(8) 20.67±0.65 [19.82–21.54]	(4) 28.46±1.6 [26.22–29.65]
Coracoid				
Medial length (A)	(8) 40.15±1.36[38.56–42.16]	(9) 41.64±1.67 [38.77–43.59]	(8) 35.09±0.50 [34.22–35.78]	(9) 50.40±1.87 [47.62–52.98]
Depth of acrocoracoid (B)	(8) 7.07±0.30 [6.61–7.51]	(9) 7.83±0.50 [7.05–8.4]	(8) 6.26±0.32 [5.83–6.81]	(9) 9.35±0.48 [8.45–10.22]
Width of acrocoracoid (C)	(8) 5.42±0.24 [5.2–5.83]	(9) 6.03±0.37 [5.43–6.52]	(8) 4.72±0.18 [4.47–4.94]	(9) 7.41±0.68 [6.92–9.16]
Width of shaft at procoracoid (D)	(8) 8.26±0.44 [7.45–8.72]	(9) 8.67±0.67 [7.36–9.6]	(6) 6.75±0.18 [6.46–6.94]	(2) [10.21–10.73]
Scapula				
Articular length (A)	(8) 11.46±0.35 [10.9–11.95]	(9) 12.66±0.56 [11.98–13.61]	(7) 9.33±0.79 [7.83–10.12]	(4) 14.29±2.13 [11.31–16.24]
Length of Fac. artic. humeralis (B)	(8) 7.26±0.25 [6.7–7.48]	(9) 7.5±0.43 [6.9–8]	(7) 6.23±0.33 [5.79–6.7]	(4) 8.98±0.62 [8.46–9.86]
Width of Fac. artic. humeralis (C)	(8) 5.32±0.21 [5.01–5.64]	(9) 5.59±0.45 [4.66–6.18]	(7) 4.85±0.17 [4.59–5.12]	(4) 6.39±0.49 [5.7–6.85]
Humerus				
Total length (A)	(14) 99.7±2.29 [95.84–103.81]	(7) 105.38±2.72 [101.87–108.77]	(19) 86.20±2.26 [81.05–90.95]	(8) 132.58±4.3 [126.32–137.71]
Proximal width (B)	(14) 16.97±0.53 [16.25–17.98]	(7) 18.19±0.81 [17.02–19.31]	(8) 15.23±0.43 [14.37–15.64]	(8) 22.35±0.75 [21.25–23.36]
Distal width (C)	(14) 17.11±0.39 [16.43–17.76]	(7) 17.46±0.92 [16.25–19.18]	(8) 15±0.33 [14.39–15.5]	(8) 22.14±0.94 [20.69–23.26]
continued …				continued …

Table 1 continued. Measurements (mm) of skeletal elements of the late Pleistocene *Oraristrix brea* compared with extant species and fossil *Bubo virginianus* from Rancho La Brea (see Figs 10 and 11 for illustrations of measurements). Measurements given in the order: (number of specimens) arithmetic mean ± standard deviation [observed range].

Measurements	*Strix occidentalis*	*Strix varia*	*Strix aluco*	*Strix nebulosa*
Radius				
Total Length (A)	(8) 104.06±1.87 [101.47–106.97]	(8) 109.35±3.16 [105–113.76]	(8) 89.85±1.27 [87.65–91.9]	(8) 135.79±4.6 [129.53–140.83]
Maximum proximal width (B)	(8) 6.19±0.29 [5.75–6.51]	(8) 5.86±1.38 [3.44–6.99]	(8) 5.46±0.15 [5.3–5.66]	(8) 7.91±0.52 [7.18–8.48]
Minimum proximal width (C)	(8) 3.79±0.12 [3.55–3.91]	(8) 4.59±1.18 [3.61–6.64]	(8) 3.19±0.18 [3.02–3.55]	(8) 4.75±0.28 [4.28–5.01]
Distal width (D)	(8) 8.63±0.36 [8.16–9.27]	(8) 8.56±0.5 [7.75–9.2]	(8) 7.46±0.33 [7.01–7.88]	(8) 10.75±0.41 [9.93–11.23]
Ulna				
Total Length (A)	(11) 108.59±1.99 [106.37–112.64]	(8) 114.87±3.25 [110.43–119.61]	(19) 94.01±2.66 [86.81–99.83]	(8) 142.72±5.08 [135.75–148.46]
Proximal width (B)	(11) 10.58±0.39 [9.97–11.09]	(8) 10.99±0.51 [10.33–11.98]	(8) 9.45±0.26 [9.06–9.78]	(8) 13.65±0.53 [12.92–14.22]
Proximal depth (C)	(11) 8.56±0.37 [7.97–9.05]	(8) 8.97±0.48 [8.39–9.67]	(8) 7.44±0.16 [7.17–7.71]	(8) 11.56±0.38 [10.83–12.05]
Width of Condylus dorsalis (D)	(11) 8.88±0.39 [8.3–9.43]	(8) 9.02±0.58 [8.47–10.21]	(8) 7.62±0.71 [6.52–8.8]	(8) 10.55±0.52 [9.48–11.03]
Carpometacarpus				
Total length (A)	(6) 50.06±1.69 [47.79–51.99]	(8) 53.85±1.9 [50.68–56.96]	(19) 44.74±1.21 [42.51–47.20]	(8) 64.98±3.01 [60.06–68.24]
Proximal width (B)	(6) 11.97±0.38 [11.54–12.59]	(8) 11.86±0.48 [11.22–12.66]	(8) 10±0.27 [9.63–10.34]	(8) 14.81±0.62 [13.61–15.61]
Proximal depth (C)	(6) 6.08±0.36 [5.7–6.68]	(8) 6.42±0.25 [6.08–6.81]	(8) 5.26±0.19 [4.91–5.47]	(8) 7.77±0.36 [7.28–8.37]
Depth of mid-shaft (D)	(6) 3.73±0.17 [3.52–3.91]	(8) 4.04±0.08 [3.89–4.13]	(8) 3.54±0.15 [3.37–3.76]	(8) 5.41±0.24 [5.04–5.66]
Distal width (E)	(6) 9.8±0.36 [9.37–10.29]	(8) 9.81±0.63 [9.12–10.98]	(8) 8.27±0.35 [7.64–8.66]	(8) 11.66±0.61 [10.88–12.58]
Pelvis				
Neural arch height (A)	(12) 8.39±0.73 [7.36–9.28]	(9) 9.68±0.67 [8.92–10.88]	(8) 7.34±0.29 [6.9–7.61]	(4) 12.19±1.24 [10.59–13.63]
Centre height through vertebra (B)	(12) 15.07±0.69 [14.01–16.29]	(9) 16.43±0.85 [15.47–17.57]	(8) 13.05±0.4 [12.21–13.42]	(4) 20.26±1.42 [18.33–21.75]
Width through prezygapop (C)	(12) 7.9±0.17 [7.68–8.23]	(9) 8.02±0.31 [7.6–8.48]	(8) 7.5±0.16 [7.27–7.78]	(4) 10.35±0.99 [9.39–11.63]
Width through antitrochanter (D)	(12) 31.83±1.18 [29.85–33.73]	(8) 33.21±1.94 [30.86–35.2]	(7) 27.93±1 [26.93–29.8]	(4) 38.67±1.79 [36.74–41.06]
Width through 1st transverse process (E)	(12) 15.53±0.61 [14.73–16.52]	(9) 17.43±0.58 [16.72–18.35]	(8) 14.88±0.36 [14.44–15.44]	(4) 21.7±1.89 [19.2–23.54]
Femur				
Medial length (A)	(15) 64.41±1.58 [62.27–67.17]	(8) 70.11±1.48 [67.56–72.2]	(19) 59.05±1.93 [55.45–91.92]	(9) 85.04±2.68 [82.35–90.33]
Proximal width (B)	(15) 11.87±0.36 [11.25–12.32]	(7) 13.42±0.62 [12.83–14.4]	(8) 10.82±0.2 [10.51–11.09]	(9) 15.77±0.72 [14.73–16.77]
Width at mid-shaft (C)	(15) 5.13±0.16 [4.88–5.44]	(8) 5.73±0.32 [5.36–6.28]	(8) 4.5±0.17 [4.22–4.75]	(9) 6.47±0.41 [5.65–6.95]
Depth at mid-shaft (D)	(15) 4.91±0.26 [4.51–5.48]	(8) 5.39±0.34 [4.99–5.83]	(8) 4.59±0.18 [4.36–4.81]	(9) 6.72±0.15 [6.48–6.95]
Distal width (E)	(15) 12.29±0.46 [11.67–13.07]	(8) 13.51±0.82 [12.62–14.92]	(8) 11.21±0.42 [10.73–11.83]	(9) 16.79±0.85 [15.19–17.34]
Distal depth (F)	(15) 9.86±0.31 [9.45–10.42]	(8) 11.4±0.54 [10.75–12.27]	(8) 9.19±0.64 [7.88–9.84]	(9) 14.39±0.76 [12.81–15.25]
Tibiotarsus				
Total length (A)	(8) 96.27±2.05 [93.56–98.74]	(8) 105.62±2.28 [102.23–108.14]	(19) 86.15±2.59 [79.33–91.92]	(8) 118.99±3.85 [114.5–125.8]
Proximal width (B)	(8) 10.97±0.27 [10.53–11.33]	(8) 11.38±0.61 [10.72–12.31]	(8) 9.63±0.43 [9.14–10.34]	(8) 13.78±0.64 [12.91–14.66]
Proximal depth (C)	(8) 12.26±0.52 [11.49–12.96]	(8) 13.16±0.7 [12.54–14.53]	(8) 11.29±0.44 [10.76–11.86]	(8) 16.21±0.62 [15.1–16.94]
Width at mid-shaft (D)	(8) 4.94±0.13 [4.79–5.14]	(8) 5.42±0.3 [4.98–5.98]	(8) 4.5±0.12 [4.29–4.72]	(8) 6.14±0.29 [5.65–6.55]
Distal width (E)	(8) 11.38±0.36 [10.81–11.73]	(8) 11.91±0.79 [11.08–13.17]	(8) 9.77±0.31 [9.33–10.16]	(8) 14.49±0.49 [13.5–14.98]
Cond. lateralis depth (F)	(8) 9.24±0.26 [8.81–9.55]	(8) 9.88±0.39 [9.45–10.48]	(8) 8.07±0.18 [7.72–8.24]	(8) 11.85±0.67 [10.61–12.45]
Cond. medialis depth (G)	(8) 9.45±0.35 [8.87–9.79]	(8) 9.99±0.34 [9.6–10.57]	(8) 8.28±0.27 [7.86–8.67]	(8) 11.73±0.58 [10.85–12.45]
Tarsometatarsus				
Total length (A)	(10) 55.04±1.08 [53.6–56.62]	(8) 57.95±2.46 [53.01–60.35]	(19) 48.62±1.13 [46.33–50.45]	(8) 57.06±2.06 [54.15–59.92]
Proximal width (B)	(10) 11.32±0.55 [10.29–11.88]	(8) 11.84±0.77 [10.99–13.09]	(3) 9.38±0.12 [9.27–9.5]	(7) 14.62±0.37 [13.99–15.2]
Length of hypotarsus (C)	(10) 5.63±0.36 [5.16–6.28]	(8) 7.37±0.57 [6.27–7.93]	(8) 6.19±0.56 [5.46–7.03]	(8) 8.09±0.6 [7.15–9.02]
Width of hypotarsus (D)	(10) 2.65±0.14 [2.32–2.84]	(8) 2.74±0.3 [2.37–3.15]	(8) 2.32±0.14 [2.05–2.47]	(8) 3.6±0.21 [3.28–3.86]
Minimum shaft width (E)	(10) 5.84±0.23 [5.53–6.2]	(8) 6.44±0.53 [5.92–7.26]	(8) 5.11±0.19 [4.97–5.51]	(8) 7.69±0.42 [6.77–8.23]
Distal width (F)	(9) 12.93±0.53 [11.87–13.56]	(8) 14.25±0.83 [13.08–15.57]	(8) 11.23±0.41 [10.71–11.87]	(8) 16.55±0.98 [14.7–17.26]

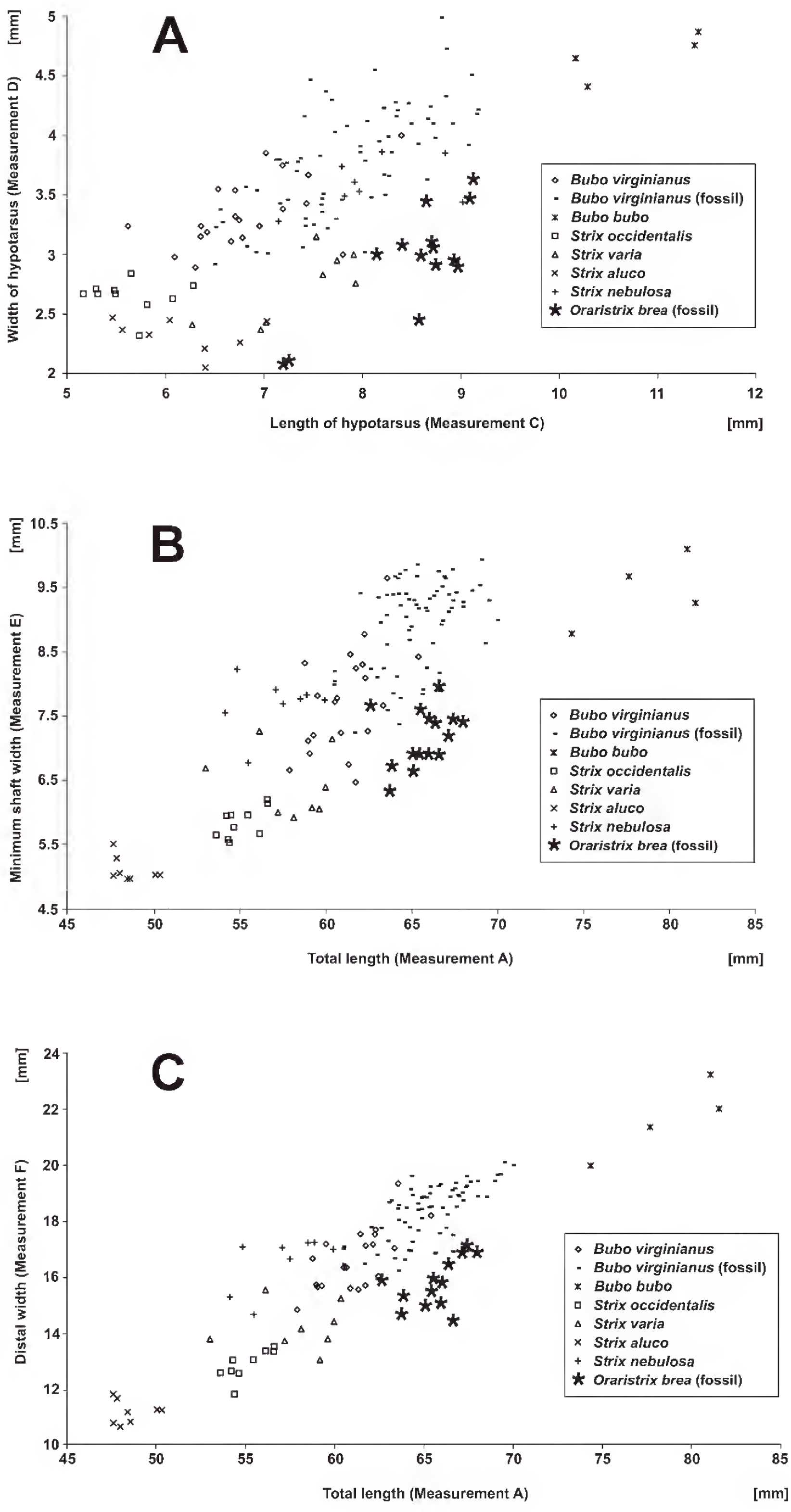


Figure 2. Intra-element proportions of the tarsometatarsus of *Oraristrix brea* distinguish it from modern species of owls. (*A*) Scatter diagram of length *vs.* width of posterior surface of hypotarsus. For its length, the posterior surface of the hypotarsus of *O. brea* is relatively narrow compared to that of modern owls. (*B*) Scatter diagram of total length *vs.* minimum shaft width of tarsometatarsus. The length of *O. brea* is within the upper values for *Bubo virginianus*, but most of the fossils have a relatively slender shaft. (*C*) Scatter diagram of total length *vs.* distal width of tarsometatarsus. The length of *O. brea* is within the upper values for *Bubo virginianus*, but most of the fossils have a relatively narrower distal end.

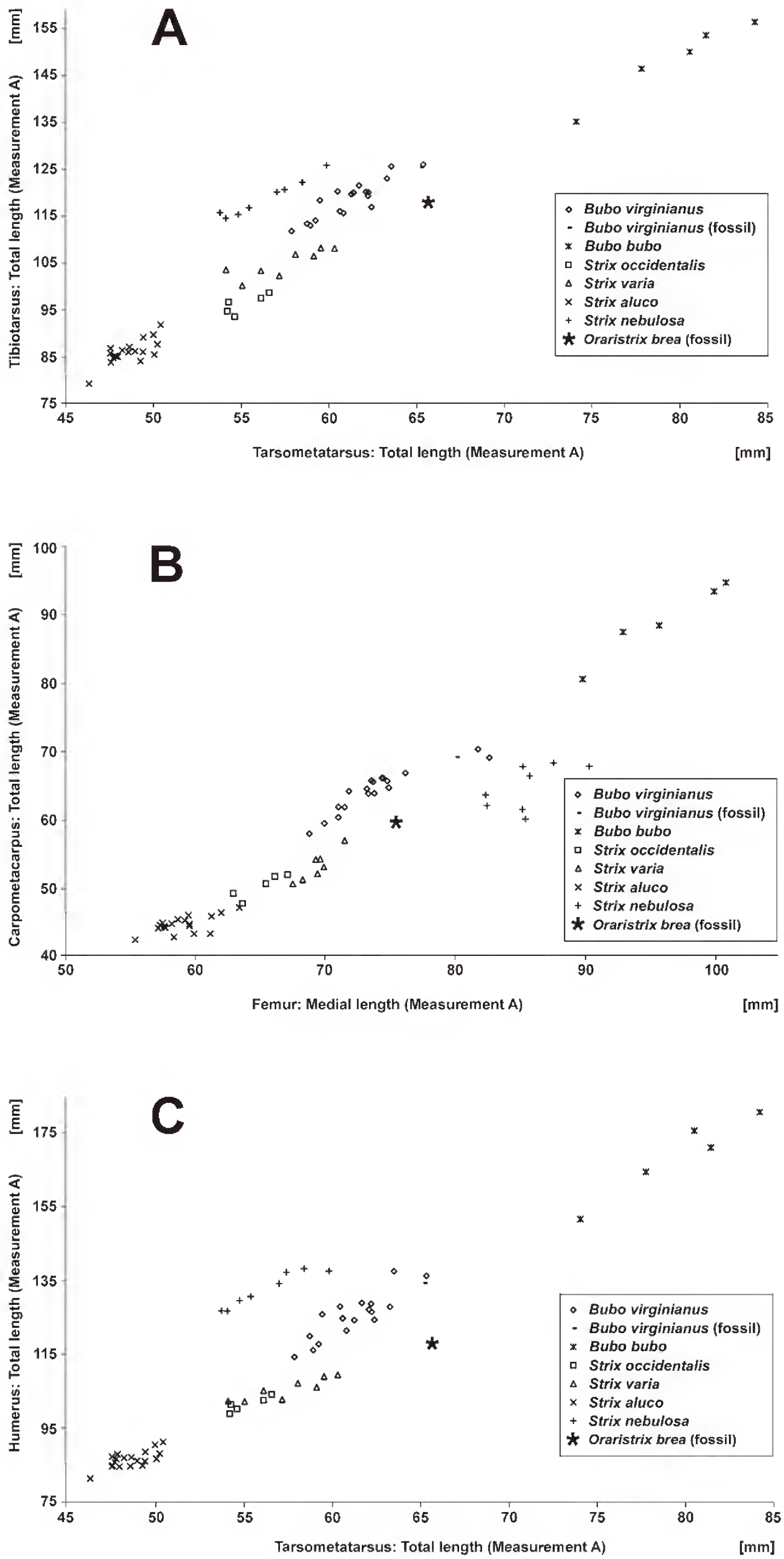
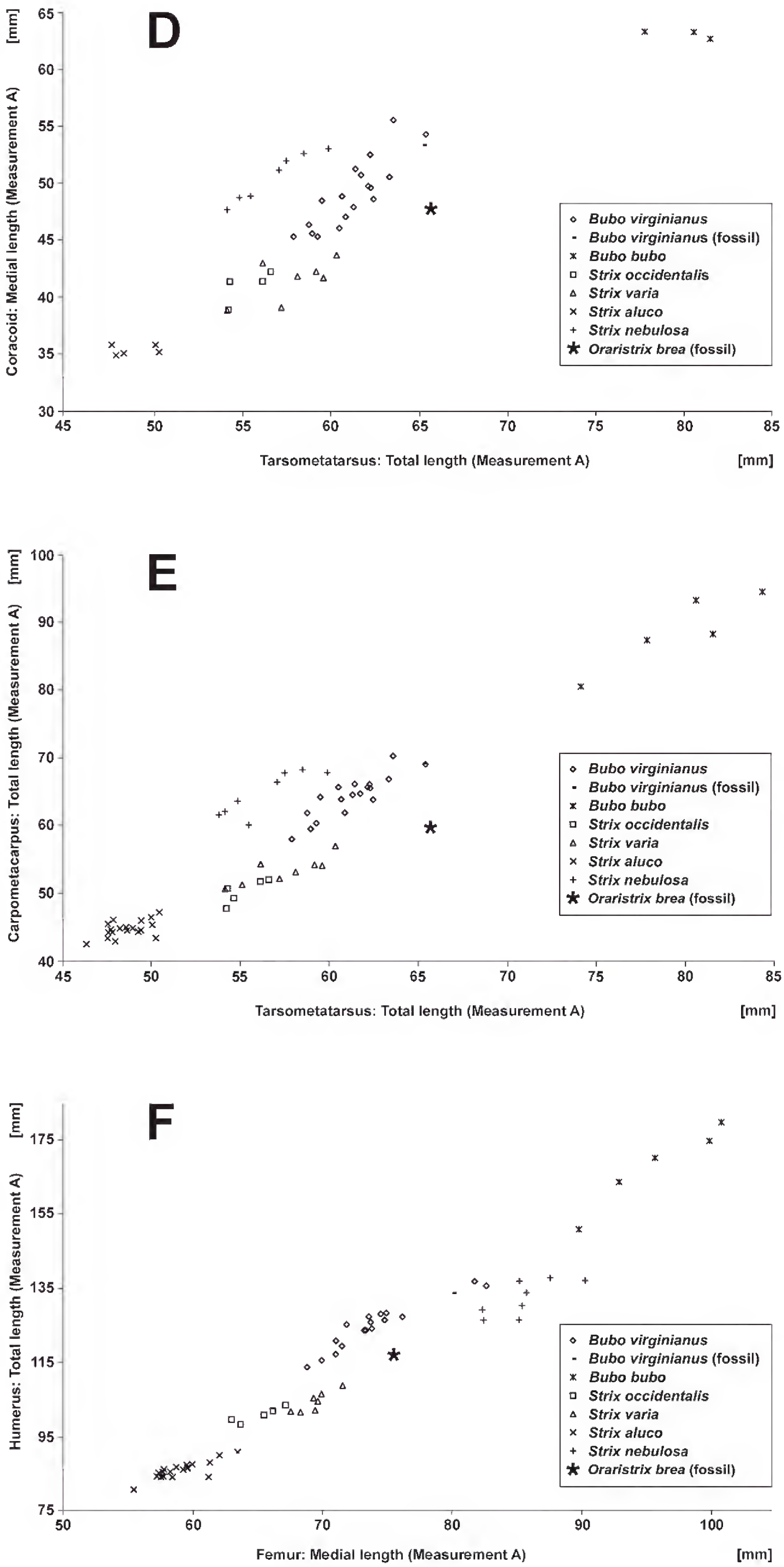


Figure 3. Intra-membral and inter-membral element plots give an indication of how *Oraristrix brea* differed from the modern owls *Bubo bubo, B. virginianus, Strix nebulosa, S. occidentalis, S. varia*, and *S. aluco*. (*A*) Tarsometatarsus length *vs.* tibiotarsus length. (*B*) Femur medial length *vs*. carpometacarpus length. (*C*) Tarsometatarsus length *vs.* humerus length. (*D*) Tarsometatarsus length *vs.* coracoid medial length. (*E*) Tarsometatarsus length vs. Carpometacarpus length. (*F*) Femur medial length vs. humeral length. For the modern species,… [continued on facing page]



[Figure 3. continued from facing page] … each symbol represents one specimen, whereas for *Oraristrix brea* and fossil *Bubo virginianus* from Rancho La Brea the symbol stands for the arithmetic means of all fossil specimens of particular elements. For *O. brea* the number of fossil specimens available for calculating the means was as follows: humerus, 4; coracoid, 10; carpometacarpus, 7; femur, 5; tibiotarsus, 5; tarsometatarsus, 15. For fossil *B. virginianus*, the number of specimens available for calculating the means was as follows: humerus, 6; ulna, 6; carpometacarpus, 34; femur, 41; tibiotarsus, 18; tarsometatarsus, 68.

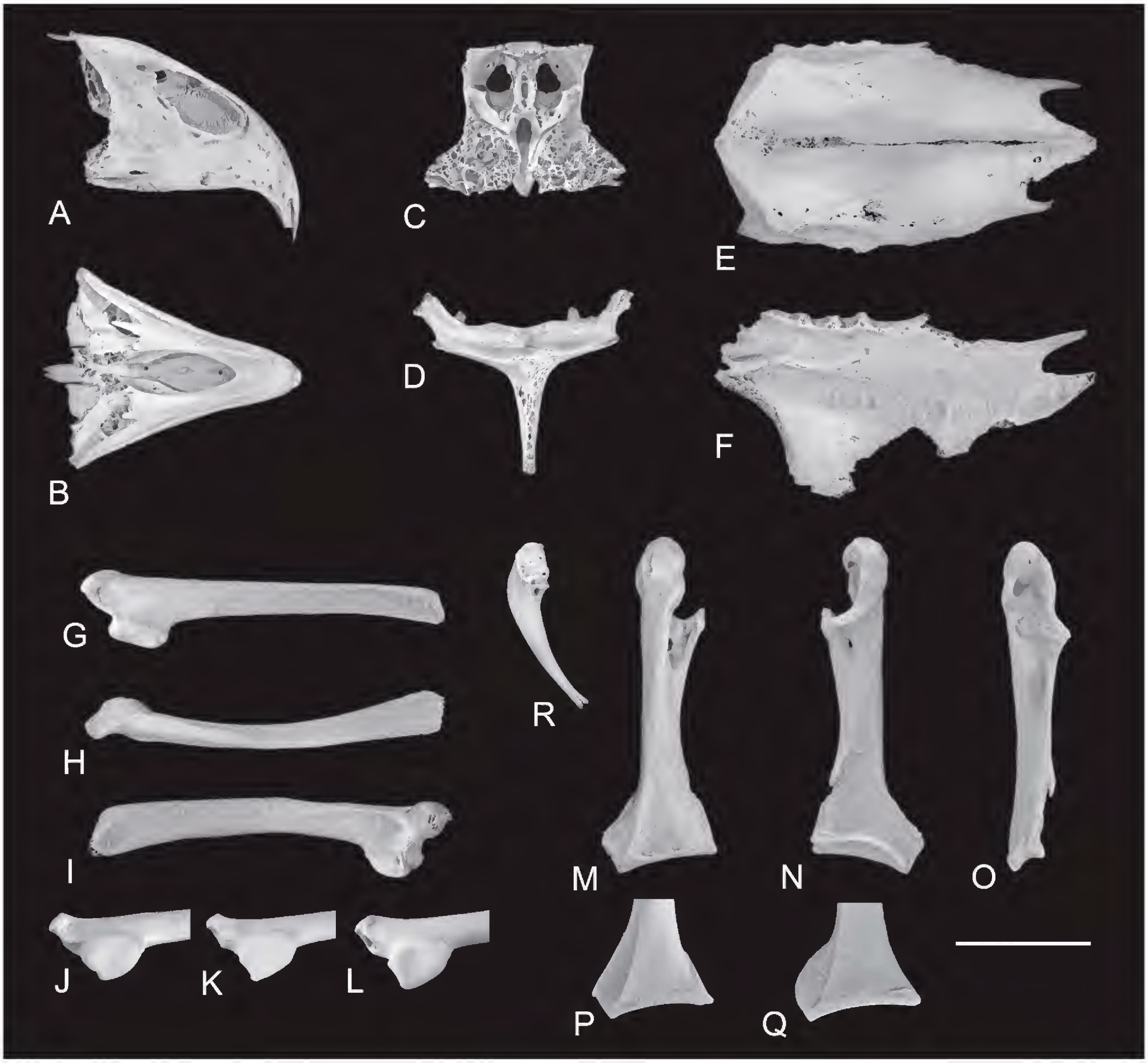


Figure 4. Rostrum maxillare of *Oraristrix brea* (LACM RLB K2713) in (*A*) lateral, (*B*) ventral, and (*C*) posterior views. Sternum of *O. brea* (LACM RLB F2477) in (*D*) anterior, (*E*) ventral, and (*F*) lateral view. Scapula, left, of *O. brea* (LACM RLB H6613), in (*G*) dorsolateral, (*H*) dorsomedial, and (*I*) ventromedial views. Close-up of glenoid facet of (*J*) *O. brea* (LACM RLB H6613), (*K*) *Bubo virginianus* (LACM 109120), and (*L*) *Strix nebulosa* (MVZ 151874) illustrating the consistent differences in the shape of this facet among the species. Coracoid, right, of *O. brea* (LACM RLB F9687), in (*M*) ventral, (*N*) dorsal, and (*O*) medial view. Sternal ends of (*P*) *B. virginianus* (LACM 109120), and (*Q*) *S. nebulosa* (MVZ 155426) illustrate the differences in their Angulus medialis. The differing placement of the Linea intermusculare and the size of the Fac. artic. sternalis can also be noted. Clavicula, left, of *O. brea* (LACM RLB E9233), in (*R*) lateral view. Scale bar = 20 mm.

separated in median line anteriorly, which we interpret as in ventral view through Concavitas maxillare) is valid for separating the Brea Owl from *Bubo virginianus* and allying it with the traditional species of *Strix*. That is, the turbinates are similar, or even less inflated in *Strix* and markedly more inflated in *Bubo*. However, available species of *Ciccaba*, a genus now included in *Strix*, have well inflated anterior turbinates. On the other hand, the anterior turbinates of *Nyctea*, a genus now included in *Bubo*, are not inflated. Although the Rostra maxillare of all large owl specimens in the Rancho La Brea collections are damaged, most of them preserve the anterior parts of the turbinates and some or all of the other characters mentioned above, and they are identifiable as either *Bubo* or *Oraristrix*.

It is interesting to note that the Rostrum maxillare of *Oraristrix brea* was nearly as tall and long as that of the living Eurasian Eagle-owl, *Bubo bubo*, which is much larger than *B. virginianus*, but it was noticeably narrower (Table 1). What this might indicate about its predatory habits is unclear, but it was a strong predator.

Sternum (Fig. 4D–F). Characterized by having (1) Linea intermusculare beginning at Tub. labri externi or posterior to it (similar in *Strix*; Linea intermusculare begins medial and anterior to Tub. labri externi in *Bubo*) (Howard, 1933); (2) Tub. labrum externi not projecting greatly laterad, resulting in only slight to moderate curvature toward midline of Labrum externi and a shallow Sulci artic. coracoideus dorsal to Tub. labrum externi (Tub. labrum externi projecting more laterad, resulting in slight to moderate curvature to Labrum externi in *Strix* and much greater curvature in *Bubo*, and a deep to very

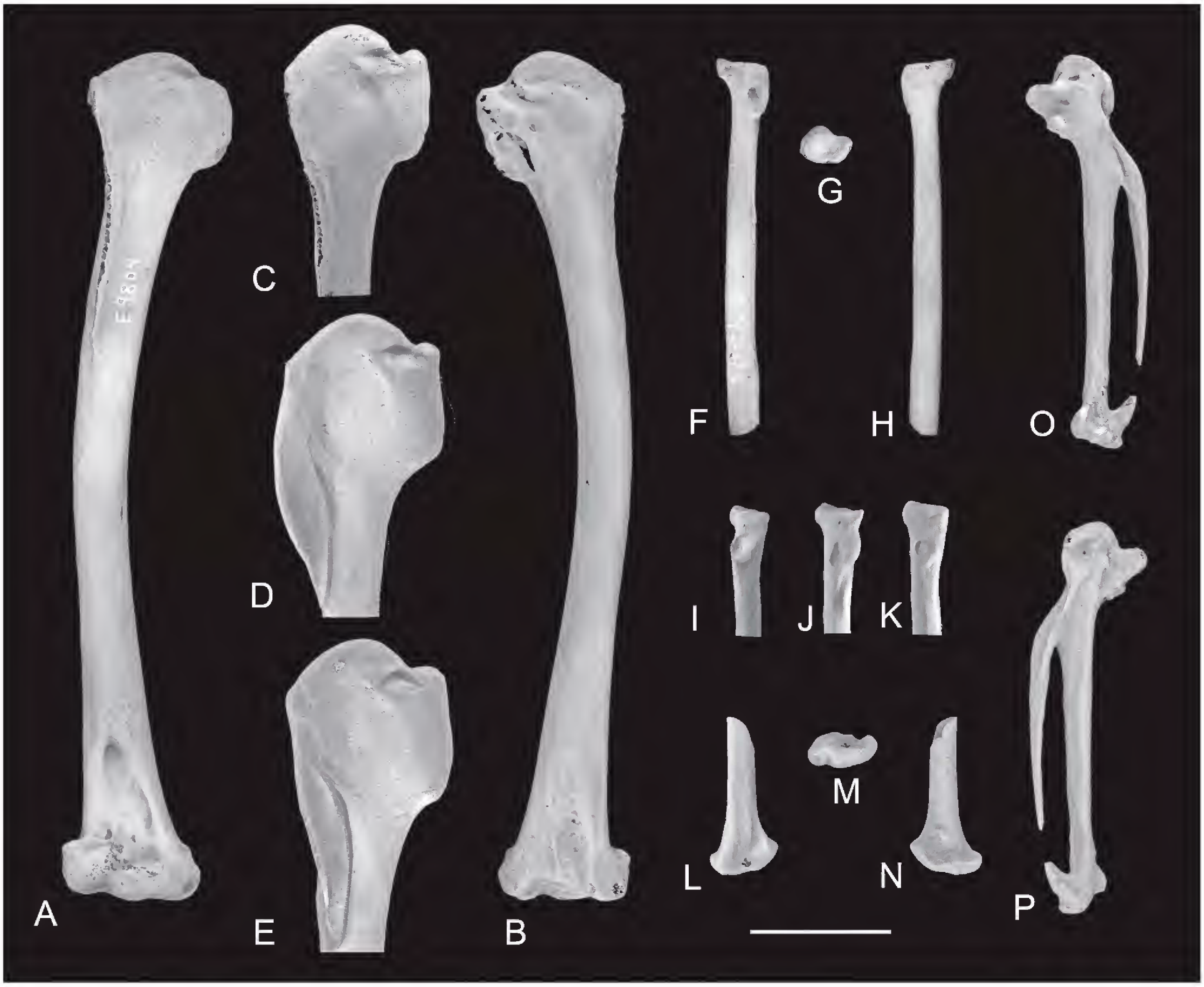


Figure 5. Humerus, right, of *Oraristrix brea* (LACM RLB E9804), in (*A*) anterior and (*B*) posterior view, and (*C*) proximal end in anteroproximal view. Anteroproximal view of proximal ends of (*D*) *Bubo virginianus* (LACM 109226), and (*E*) *Strix nebulosa* (MVZ 155426) illustrates the differences in the form of the Crista bicipitalis and the Sulcus ligamentum transversus. Radius, left, of *O. brea* (LACM RLB K9798), in (*F*) anterior, (*G*) proximal, and (*H*) posterior view. Anteroventral view of left proximal radii of (*I*) *O. brea* (LACM RLB K9798), (*J*) *S. nebulosa* (MVZ 151874), and (*K*) *B. virginianus* (LACM 109226) illustrates the differences in the form and position of the attachment for M. biceps brachii. Radius, distal end, left, of *O. brea* (LACM RLB K9627), in (*L*) dorsal, (*M*) distal, and (*N*) ventral view. Carpometacarpus, left, of *O. brea* (LACM RLB K9432), in (*O*) dorsal and (*P*) ventral view. Scale bar = 20 mm.

deep Sulci artic. coracoideus dorsal to Tub. labrum externi in both *Strix* and *Bubo*); (3) Corpus sternae with Margo posterior pointed, or arrow-shaped, and with Carina sterni extending to tip (Margo posterior of sternum in *Strix* squared off or slightly rounded, moderately wide, with Carina sterni merging before posterior end; Margo posterior of sternum in *Bubo* squared off or centrally notched, moderately wide to wide, with Carina sterni merging before posterior end). The three fossil sternae are too fragmentary to secure many accurate measurements, and minor breakage to Margo posterior of Corpus sternae might have accentuated its pointed form.

Clavicula (Fig. 4R). Characterized by having (1) Fac. artic. acrocoracoidea a moderately deep, elongated oval facing posterolaterad (facet more elongated than oval, less concave, and facing more posteriad in *Strix*; facet more oval, moderately deep, and facing more posteriad in *Bubo*); (2) Fac. artic. procoracoidea small, narrow, not well marked (facet much broader and well marked in *Strix* and *Bubo*); (3) Extremitas omalis claviculae short (long in *Strix* and *Bubo*).

Scapula (Fig. 4G–J). Characterized by having (1) acromion short, blunt-ended, and overall stout (i.e., wider dorsoventrally), in dorsolateral view (acromion much longer, narrower, and slightly less rounded anteriorly in *Bubo*; short to long, narrower, and more pointed anteriorly in *Strix*) (Howard, 1933); (2) Fac. artic. humeralis (glenoid facet) with ventral edge moderately rounded, in medial view (ventral edge nearly straight in *Bubo*; slightly to moderately rounded in *Strix*); (3) Fac. artic. humeralis more rounded than elongated (glenoid facet rounded to elongated in *Strix* and more elongated in *Bubo*); (4) medial surface just posterior to acromion markedly concave with long, prominent, narrow ridge marking dorsomedial corner of bone (area with shallow, elongated depression with long, sharp ridge narrowing posteriad in *Strix*; area with shallow depression and with short to moderately long, prominent ridge narrowing rapidly posteriad in *Bubo*). Characters (2) and (3) were combined by Howard (1933:68) when she referred to the glenoid facet of *Oraristrix brea* as "appearing more 'heart-shaped' than *Bubo* …, resembling *Strix* in this character…".

Coracoid (Fig. 4M–O). Characterized by having (1)

Figure 6. Ulna, right, of *Oraristrix brea* (LACM RLB E9544), in (*A*) anterior, (*B*) ventral, and (*C*) posterior view. Anteroproximal view of (*D*) *O. brea* (LACM RLB E9804), (*E*) *Bubo virginianus* (LACM 87413), and (*F*) *Strix nebulosa* (MVZ 155426) illustrate the differences in form of the olecranon and the position of the Tuberculum lig. coll. ventralis. Scale bar = 20 mm.

Proc. acrocoracoideus claviculae (anterior end, in ventral view) broad, narrowing sharply at Fac. artic. clavicularis [Proc. acrocoracoideus claviculae broad, narrowing slightly via curvature at Fac. artic. clavicularis in *Strix* (excluding *Ciccaba*, where it widens slightly at Fac. artic. clavicularis); Proc. acrocoracoideus claviculae broad, narrowing gradually in *Bubo* (excluding *Nyctea*, where it narrows more abruptly, but less so than in *Oraristrix*) (Howard, 1933); (2) Fac. artic. clavicularis relatively long, narrow, oriented at a slight angle to the long axis of shaft (shorter to long, a relatively narrow oval, oriented at a slightly greater angle to the long axis of shaft in *Strix*; elongated oval to broad oval, not oriented at angle to long axis of shaft in *Bubo*); (3) Proc. procoracoideus with terminus irregularly shaped, with broadened ventral half hosting a small Fac. artic. clavicularis posterior (Fac. artic. clavicularis elongated, blunt, and covering the entire end of a broad, oval Proc. procoracoideus in *Strix* and *Bubo*); (4) shaft ventrolateral to Fac. artic. humeralis gently rounded (shaft more convex in this area in *Strix* and *Bubo*) (Howard, 1933); (5) Fac. artic. sternalis shallow, or narrow, in sternal view, extending mediad beyond tip of Angulus medialis (Fac. artic. sternalis moderately deep to deep in *Strix* and *Bubo*, in sternal view, not extending mediad beyond tip of Angulus medialis); (6) Angulus medialis near 90 degrees, in ventral view (Angulus medialis, in ventral view, moderately to very angular in *Strix* and very angular in *Bubo*); (7) Linea intermusculare ventralis directly in line with Angulus lateralis of Fac. artic. sternalis (similar in *Strix*; Linea intermusculare ventralis positioned medial to Angulus lateralis of Fac. artic. sternalis in *Bubo*).

Howard (1933) described the pneumatization of the Proc. acrocoracoideus claviculae as being less pronounced in *Oraristrix brea* than in *Strix* or *Bubo*. We found this character to be quite variable, even within individuals, and we do not consider it a valid distinguishing character. Character 4 above (from Howard, 1933) is difficult to identify, and it is probably not a readily distinguishing character.

Humerus (Fig. 5A–C). Characterized by having (1) Caput humeri prominently developed ventral to Tub. dorsale (less developed in *Strix* and *Bubo*); (2) Sulcus ligamentum transversus shallow, not extending ventrad past ventral edge of Incisura capitis (extends ventrad as moderately deep groove past ventral edge of Incisura capitis in *Strix*; extends ventrad as a deep groove to well past ventral edge of Incisura capitis in *Bubo*); (3) Crista bicipitalis, in anterior view, short and not extending past ventral edge of Tub. ventrale (long and similar, or extending slightly past ventral edge of Tub. ventrale, in *Strix*; long and extending slightly to well past ventral edge of Tub. ventrale in *Bubo*); (4) Epicondylus dorsalis with prominent spur proximal to proximal end of Condylus dorsalis (similar to very prominent spur at, or just proximal to, proximal end of Condylus dorsalis in *Strix*; very prominent spur, proximal to proximal end of Condylus dorsalis in *Bubo*).

Although Howard (1933) noted a somewhat larger Foramen pneumaticum in *Strix* than in *Bubo*, we found too much variability in this character to consider it reliable. We could not discern the "difficult to describe" differences in form of the attachment of M. brachialis mentioned by Howard (1933:68).

Ulna (Fig. 6A–D). Characterized by having (1) olecranon short, or moderately produced proximad, without proximal end turning ventrad, in anterior view (olecranon short in *Strix*, but with proximal end turning ventrad; olecranon moderate to long in *Bubo*, with proximal end turning ventrad); (2) Tub. lig. coll. ventralis relatively close to rim of Cotyla ventralis (moderate to large distance from rim of Cotyla ventralis in *Strix* and *Bubo*). Howard (1933) did not describe the ulna of *Oraristrix brea*.

Radius (Fig. 5F–I, L–N). Characterized by (1) attachment for M. biceps brachii large, located mostly on posterior side of shaft at a moderate distance from Cotyla humeralis (similar in size, positioned more dorsally, or externally, on

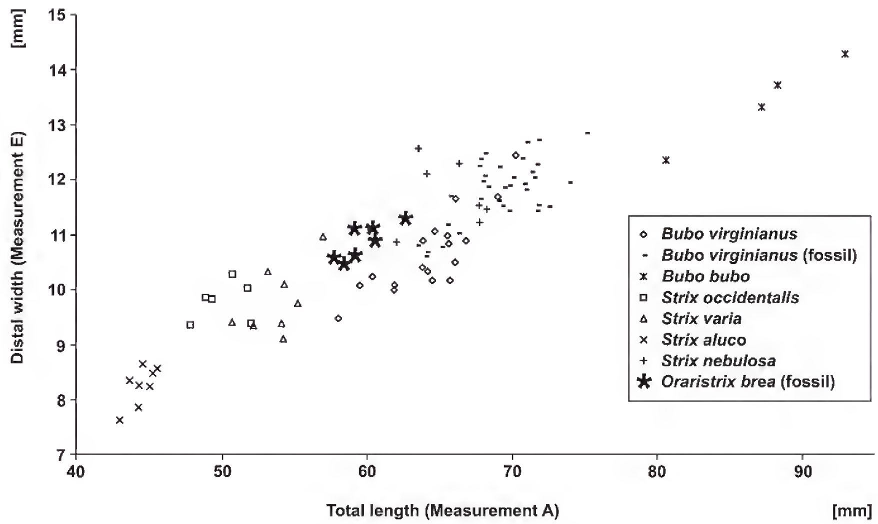


Figure 7. A scatter plot of total length *vs.* distal width of the carpometacarpus of *Oraristrix brea* suggests that this bone had a stout distal end in comparison with that of *Bubo virginianus*, with some overlap with that of *Strix nebulosa*.

shaft and farther from Cotyla humeralis in *Bubo*; attachment area similar in size but with external rim significantly larger, positioned more toward dorsal side of shaft, and at a greater distance from Cotyla humeralis in *Strix*); (2) Cotyla humeralis narrow and elongated (broader and more oval in *Bubo* and *Strix*); (3) distal end with Tub. aponeurosis ventralis short and distinctly set off from edge of shaft, in dorsal view [more elongated and slightly less distinctly set off from edge of shaft in *Strix*; more elongated and not distinctly set off from edge of shaft (i.e., connected to edge of shaft by a long curve) in *Bubo*]. Howard (1933) did not describe the radius of *Oraristrix brea*.

Carpometacarpus (Figs 5O–P, 7). Characterized by having (1) Fac. artic. ulnocarpalis of Trochlea carpalis with ventral portion relatively narrow for length, moderately inflated posterodistally, in posterior view (wider and more inflated posterodistally in *Strix* and *Bubo*); (2) Fac. artic. ulnocarpalis of Trochlea carpalis with posterodistal rim fairly straight, in dorsal view (Fac. artic. ulnocarpalis with posterodistal rim rounded and extending farther posteriad in *Strix* and *Bubo*); (3) Tuberositas metacarpi majoris rounded in anterior view, distinctly set off from shaft proximally (rounded to triangular in *Strix*, less distinctly set off from shaft proximally; triangular shaped in *Bubo*, less distinctly set off from shaft proximally); (4) Os metacarpale minus with a distinct ridge for attachment of M. interosseous ventralis distally (ridge present, but sometimes interrupted in places in *Strix*; ridge absent in *Bubo*) (modified from Howard, 1933); (5) Fac. artic. digitalis minor long, dorsoventrally (relatively slightly longer and more slender in *Strix*; shorter and more robust, or broader, in *Bubo*); (6) area anteroproximal to Fac. artic. digitalis minor (i.e., proximal dorsal symphyseal area between Os metacarpale minus and Os metacarpale majus) flattened, in dorsal view (relatively flattened in *Strix*; narrower and more convex in *Bubo*) (Howard, 1933).

Pelvis (Fig. 8A–C). Characterized by having (1) Os ischium with posterior portion short, tapering rapidly to an angular end (long, tapering gradually to a narrow point in *Bubo* and *Strix*); (2) parapophyses of lumbar and sacral vertebrae robust structures, in ventral view (parapophyses lightly built in *Bubo* and *Strix*).

Femur (Fig. 8F–I). Characterized by having (1) Crista trochanteris merging smoothly with shaft anterodistally, in lateral view (similar in *Strix*; Crista trochanteris merges abruptly with shaft in *Bubo* because its distal end is undercut); (2) attachment of M. iliotrochantericus posterior long, narrow, and located near centre of lateral side of proximal end (attachment shorter, broader, and located near posterior edge of lateral side of bone in *Strix*; longer, narrow, and centrally positioned on side of bone in *Bubo*); (3) Condylus medialis, in posterior view, with lateral end moderately undercut (condyle with lateral end more distinctly undercut, in posterior view, in *Strix* and *Bubo*); (4) Condylus lateralis, in posterior view, as wide as or wider than Trochlea fibularis (similar in *Strix*; condyle narrower than trochlea in *Bubo*); (5) proximal attachment for Impressiones ansae m. iliofibularis (biceps loop) centrally located on lateral side of shaft (centrally to anteriorly located in *Strix*) (Howard, 1933); (6) Crista lateralis of Sulcus intercondylaris immediately anterior to Fovea tendineus m. tibialis anterior not projecting distad to distal edge of, or beyond, Condylus lateralis (similar in *Strix*; projects distad nearly equal to or slightly beyond Condylus lateralis in *Bubo*); (7) Crista lateralis of Trochlea fibularis, in lateral view, well-rounded (Crista lateralis similar to elongated in *Bubo*; less rounded, more elongated posteriad in *Strix*); (8) Condylus lateralis with axis at a significant angle to long axis of shaft (Condylus lateralis nearly parallel with long axis of shaft in *Strix* and *Bubo*); (9) Fovea fibularis broadly and moderately to deeply excavated into lateral side of Condylus lateralis (Fovea fibularis a small, moderate to deep pit not excavated into side of Condylus lateralis in *Bubo* and a moderately deep pit with a portion slightly excavated into side of Condylus lateralis in *Strix*).

Although Howard (1933) correctly noted that in *Bubo virginianus* the proximal attachment for Impressiones ansae m. iliofibularis was located near the anterior edge of the shaft, and was useful for distinguishing *Oraristrix brea* and *B. virginianus*, this character did not hold up well as a generic character when other species of *Bubo* were examined.

Tibiotarsus (Fig. 8L–O). Characterized by having (1) Crista cnemialis anterior extending only slightly proximad of Crista patellaris (similar in *Strix*; extends significantly more

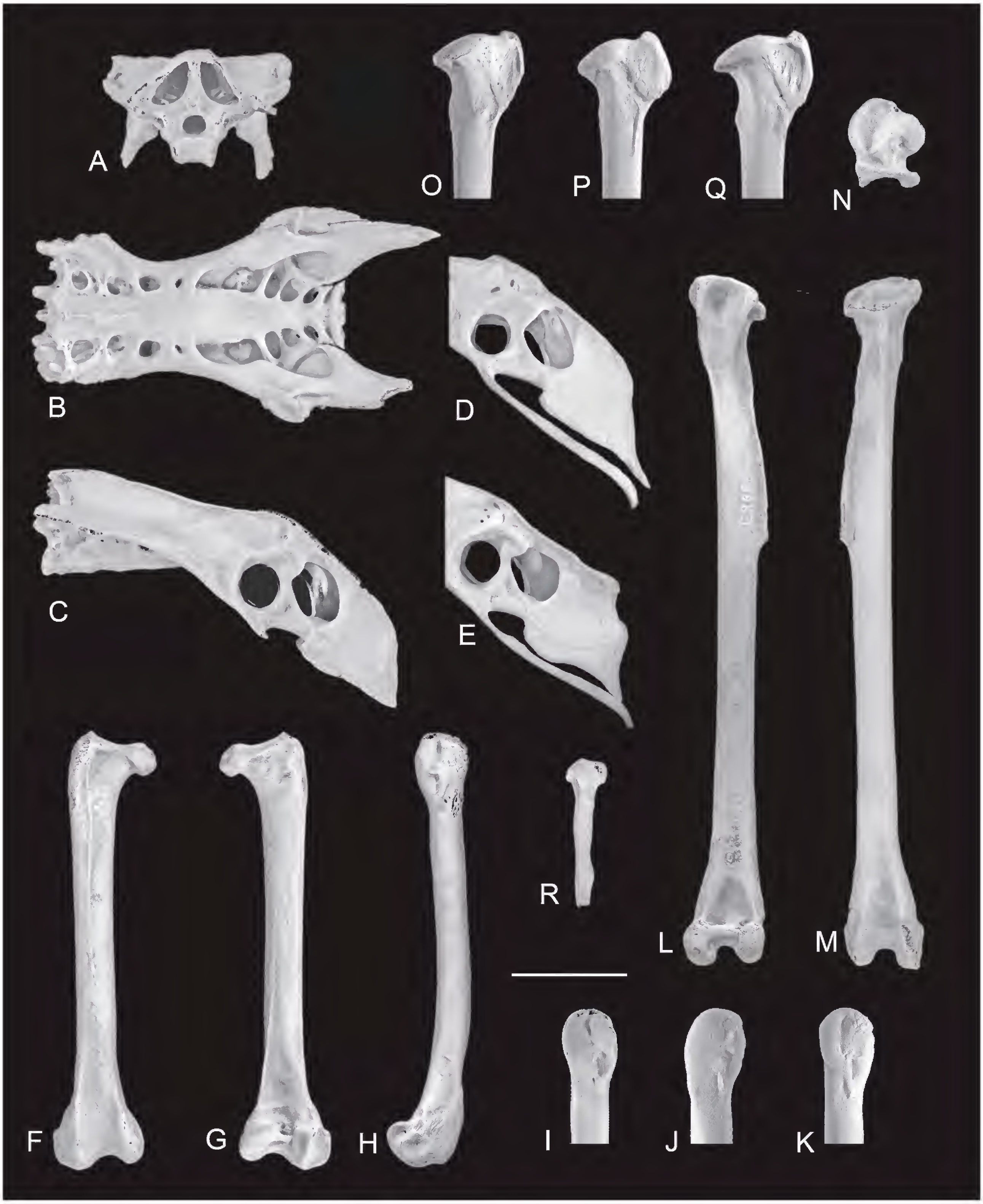


Figure 8. Synsacrum of *Oraristrix brea* (F3700) in (*A*) anterior, (*B*) ventral, and (*C*) lateral view. Views of the posterior ischium of (*D*) *Bubo virginianus* (LACM 110180) and (*E*) *Strix nebulosa* (MVZ 151874) illustrate the differences in the posterior ends of this bone in these species. There is no breakage to the posterior ischium of *O. brea*. Femur, right, of *O. brea* (K9427) in (*F*) anterior, (*G*) posterior, and (*H*) lateral view. Lateral views of the left proximal femur of (*I*) *O. brea* (K9428), (*J*) *S. nebulosa* (MVZ 155426), and (*K*) *B. virginianus* (LACM 109226) illustrate the differences in form of the Crista trochantericus and position of the attachment of M. iliotrochantericus posterior. Tibiotarsus, left, of *O. brea* (E9888) in (*L*) anterior, (*M*) posterior, and (*N*) proximal view. Medial views of left proximal tibiotarsi of (*O*) *O. brea* (E9888), (*P*) *B. virginianus* (LACM 109226), and (*Q*) *S. nebulosa* (MVZ 155426) illustrate the differences in form of the Crista cnemialis anterior and the size and position of the attachment of M. gastrocnemius, pars interna. Fibula, left, of *O. brea* (H9244) in (*R*) lateral view. Scale bar = 20 mm.

proximad in *Bubo*); (2) Fac. artic. medialis with medial and posterior edge well rounded, in proximal view (less rounded and projecting much more posteriad in *Strix* and *Bubo*); (3) Crista cnemialis lateralis long and deeply excavated, or concave, on lateral side (lateral cnemial crest similar in length and excavation in *Strix*; shorter and less excavated in *Bubo*); (4) M. gastrocnemius, pars interna, with distal attachment scar very broad, short, not extending distal to Crista cnemialis anterior (not as broad, longer, extending short distance distal to Crista cnemialis anterior in *Strix*; narrow, very long, extending considerable distance distal to Crista cnemialis anterior in *Bubo*) (Howard, 1933); (5) Fac. artic. lateralis broadened laterally, with relatively low profile (i.e., sloping less steeply laterad), in posterior view (narrower, with much higher profile in *Strix* and *Bubo*); (6) Fac. artic. medialis with flattened anterolateral corner and, in posterior view, no notch between it and Fac. artic. lateralis (facet with anterolateral corner projecting prominently proximad in *Strix* and *Bubo*, with a notch between Fac. artic. medialis and Fac. artic. lateralis); (7) Sulcus extensorius with distal portion (i.e., just proximal to Incisura intercondylaris) deeply and broadly excavated (sulcus generally deep, but slightly less broadly excavated in *Strix*; moderately deep and less broadly excavated in *Bubo*).

Howard (1933:68) stated that she found there was less angular difference present in *Strix* relative to *Bubo* between lines drawn tangent to the proximal and distal edges of the condyles. With additional species and a larger series of comparative material we found this character too variable and difficult to quantify to be reliable for distinguishing genera.

Fibula (Fig. 8R). Characterized by having (1) Caput fibulae without obvious sulcus posterior to lateral tuberosity (sulcus better developed in *Strix* and very well developed in *Bubo*); (2) Caput fibulae deeply excavated anteriorly, with anteromedial corner undercut (deeply, but not as broadly, excavated anteriorly in *Strix*, with anteromedial corner not undercut; robust anteriorly, only slightly concave and not undercut anteriorly in *Bubo*); (3) posterior flange with posteromedial corner rounded, not ending in a pointed protuberance (posteromedial corner ends in a pointed or blunt protuberance in *Strix* and *Bubo*).

Discussion

Comparison with *Grallistrix*. *Grallistrix* Olson & James, 1991, an extinct genus found in the Hawaiian Islands, was interpreted as being derived from *Strix*. *Grallistrix* was diagnosed on the basis of skull characters and the fact that it was a long-legged owl, with a wing length:leg length ratio much different from that of *Strix*. Based on the published illustrations (Olson & James, 1991), *Grallistrix* differs from *Oraristrix* by having a short, broad Crista medialis hypotarsi of the tarsometatarsus, a very angular Angulus medialis of the coracoid, and a more rounded Crista bicipitalis of the humerus that extends ventrad past the ventral edge of the Tub. ventrale, in anterior view. There are undoubtedly many other distinguishing characters, but those listed are the most obvious from the illustrations. The wing length:leg length ratios (humerus + ulna + carpometacarpus : tibiotarsus + tarsometatarsus) of the species of *Grallistrix* are also significantly different than that of *Oraristrix*, being 1.13:1 in *G. orion*; 1.05:1 in *G. geleches*; 1.10:1 in *G. erdmani*, and 1.71:1 in *Oraristrix brea*.

Osteological characters. We identified 138 specimens of *Oraristrix brea* in the Rancho La Brea collections, more than double the 56 specimens identified by Howard (1933). The greater number is a result of additional collections being available and the recognition of additional elements of the skeleton of *O. brea*. The large number of specimens brings out one of the notable attributes of the Rancho La Brea collections, which is that the number of specimens preserved is so great, it is often possible to identify a fairly large number of specimens of extinct species. When all of the major post-cranial bones are available for study it is possible to place osteological characters into a larger context. That is, if a distinctive osteological character is found on one bone, it is sometimes possible to relate it to a distinctive osteological feature on the bone(s) with which it articulates. This ability to trace features from one bone to another was also useful in our study of the extinct California Turkey, *Meleagris californica* (Bocheński & Campbell, 2006).

For *Oraristrix brea*, we noted the following correlations. On the sternum, the Tub. labrum externi does not project very far laterad, which leads to a shallow Sulcus artic. coracoideus. This, in turn, leads to a shallow, or narrow, Fac. artic. sternalis of the coracoid. From this one might infer that the articulation between the coracoid and sternum in *Oraristrix* might have been more flexible than in *Strix* or *Bubo* because the coracoid was not set as deeply into the Sulcus artic. coracoideus as it is in the latter two genera.

The anterior end of the Linea intermuscularis of the sternum begins at the Tub. labrum externi, or posterior to it, in *Oraristrix* and *Strix*, whereas in *Bubo* the anterior portion of the intermuscular line is shifted mediad. The more lateral position of the sternal intermuscular line in *Oraristrix* and *Strix* is reflected in the more lateral position of the Linea intermuscularis ventralis of the coracoid in those genera, which is directly in line with the tip of the Angulus lateralis of the coracoid. In *Bubo*, this intermuscular line lies medial to the Angulus lateralis of the coracoid.

The relatively long and narrow Fac. artic. clavicularis of the coracoid of *Oraristrix*, which is oriented at a slight angle to the long axis of the bone, is reflected in the shape and orientation of the Fac. artic. acrocoracoidea of the clavicula. Also, the lack of a broad, blunt articular facet at the terminus of the Proc. procoracoideus of the coracoid is reflected in the weak, poorly developed Fac. artic. procoracoidea of the clavicula, in contrast to the larger, and presumably stronger, articulation of the procoracoid with the clavicula in *Bubo* and *Strix*.

On the femur of *Oraristrix*, the wide Condylus lateralis is reflected in the broad, relatively low profile of the Fac. artic. lateralis of the tibiotarsus. The size and shape of the Condylus medialis of the femur in *Strix* and *Bubo* is reflected in the more elongated shape, anteroposteriorly, of the Fac. artic. medialis of the tibiotarsus, which is more rounded in *Oraristrix*. The enlarged Fovea fibularis excavated into the lateral side of the Condylus lateralis of *Oraristrix* might result from the lack of a pointed protuberance of the posteroproximal corner of the fibula, as seen in *Strix* and *Bubo*, where the Fovea fibularis is a small to moderately large, deep pit into which the protuberance of the fibula inserts. These character combinations, along with a unique placement of the distal attachment of the M. gastrocnemius, pars interna, the differential between the distal extension of the Condylus lateralis and Condylus medialis, and the greater rounding of the Crista lateralis of the Trochlea fibularis are all suggestive that the knee joint of *Oraristrix* was adapted for a different range of motion, either in locomotion or predation, than *Strix* and *Bubo*.

Size and weight. Howard (1933) observed that the bones of *Oraristrix* were generally more slender than those of *Bubo* and *Strix*. This difference can be observed in scatter diagrams for the tarsometatarsus (Fig. 2). In addition to the bone dimension differences, the differences among the three large owls can now be reasonably estimated by using observed weights of *B. virginianus* and *S. nebulosa* and the calculated weight for *O. brea*. Using the results of a study of the relationship of hindlimb bone dimensions to weight in birds by Campbell & Marcus (1992), the weight of *O. brea* can be calculated using the formula for ordinary least-squares regression: $log(y) = 2.548 \cdot log(x) – 0.414$, where y = mass in grams and x = least shaft circumference of femur in mm. The slope and intercept figures are specifically for the data subset "PB," or predatory birds, of Campbell & Marcus (1992: table 3). The results, when treating the fossil femora of *O. brea* as individuals, have a range of 792–974 g (x = 868, n = 7). When the fossil femora are treated as a population and the mean of the least shaft circumference of the seven femora is used in the formula $log(y) = 2.639 \cdot log(x) – 0.517$ (Campbell & Marcus, 1992: table 3), the estimate for the mass of the extinct owl is 900 g. These estimates fall within the low range of observed masses of 680–1450 g (♂) or 1000–2500 g (♀) for *B. virginianus* (Marks *et al.*, 1999) [average masses of various data sets cited in Houston *et al.* (1998) range from 914 to 1318 g (♂) and 1142 to 1769 g (♀)]. Bull & Duncan (1993) cite masses of 825–1050 g (n = 21, x = 890.5) (♂) and 1025–1700 g (n = 63, x = 1267) (♀) for *S. nebulosa*. As a test, we used the first equation above and the least shaft circumference of the femora of the comparative specimens of *S. nebulosa* used in this study, which were without recorded mass, to estimate the mass of *S. nebulosa*. The results were 764–1047 g (x = 970, n = 9). These figures fall within the low part of the mid-range of recorded mass for this species. These results (i.e., mass estimates of *O. brea*), in combination with limb bone measurements, are consistent with the interpretation that *O. brea* was a more slender-bodied bird than *Bubo* or *Strix*.

Howard (1933) also noted that although the length of individual elements of the Brea Owl were closer in size to *Bubo virginianus* than to either *Strix varia* or *S. occidentalis*, in its overall proportions the resemblance was more toward *Strix*. That is, although she found that the leg bones of *Oraristrix brea* tended to be longer than those of *B. virginianus*, the wing elements and coracoid were shorter than the minimum for wing bones of *B. virginianus*. She found a close similarity between *Oraristrix* and *Strix* in ratios of one element to another, except for the coracoid, which seemed to be relatively shorter.

The additional specimens identified for *Oraristrix brea*, including a complete ulna, now allow a more detailed look at wing length versus leg length in this species. Using the mean lengths for the complete limb bones (humerus, ulna, and carpometacarpus for the wing; femur, tibiotarsus, and tarsometatarsus for the leg), we see that the leg of *O. brea* is indeed longer relative to its wingspan than in *Bubo virginianus* and the similar-sized *Strix nebulosa* (Fig. 9A). However, given that femoral length is proportional to body weight (Hertel, 1992; Hertel & Campbell, 2007) and that the femur is held nearly horizontally in birds (Campbell & Marcus, 1992), its length does not necessarily reflect on the height, or stature, of a bird. Including femoral length in the wing length:leg length ratio is comparable to including the coracoid in wing length. That is, femoral length does not affect our visual perception of the stature of a bird. A more accurate representation of the wing length:leg length proportions is gained by using the humerus, ulna, and carpometacarpus for the wing and only the tibiotarsus and tarsometatarsus for the leg (Fig. 9B). This shows a more dramatic difference between the wing length:leg length proportions in *Oraristrix* relative to those of *Strix* and *Bubo*, and it more clearly reveals the long-legged nature of this owl. From this one might conclude that *Oraristrix* was an owl more adapted for ground-dwelling in an open countryside, as opposed to a more "normal" forest owl. This difference in habitat preference might well have led to functional differences that could account for the observed structure of its knee.

Generic status of the Brea Owl. Howard (1933) placed the extinct Brea Owl in the genus *Strix* because she thought that the many osteological characters she identified resembled those of *Strix* more than those of *Bubo*. *Bubo virginianus* is present in large numbers in the Rancho La Brea collections, and initially the specimens of the Brea Owl were even identified as being from that species (Miller, 1916; Husband, 1924; Howard, 1933). The large size of the Brea Owl precluded Howard (1933) from assigning it to either *Strix occidentalis* or *S. varia*, which were the only North American species of owl referred to *Strix* when Howard described the Brea Owl. At that time, the Great Gray Owl, *Strix nebulosa*, was placed in the genus *Scotiaptex*. Although she examined at least one specimen of *S. nebulosa*, she did not comment on any similarities or differences she might have noted between that species and *S. varia* or *S. occidentalis*. She did comment that *Ciccaba*, which she also examined, resembled *Strix* in many characters, and indeed, the species of *Ciccaba* are now placed in *Strix* by some authors, as noted above.

The skeleton of the Brea Owl is an interesting mosaic of many unique osteological characters, and many osteological characters similar to those of *Bubo*, on the one hand, and those of *Strix*, on the other. Although many characters would seem to link *Oraristrix* with *Strix*, as observed by Howard (1933), others appear to link it to *Bubo*. For example, three of the four characters identified for the Rostrum maxillare are more similar to those of *Bubo* than to those of *Strix*, and the fourth is unique. Also, the many interrelated characters of the bones that comprise the knee joint are very suggestive of a mode of locomotion or prey capture in *Oraristrix* that was different from that in *Bubo* or *Strix*. Other characters, such as the narrow Rostrum maxillare, the distinctive shape of the posterior ischium, and the squared-off Angulus medialis of the coracoid, appear to be unique to *Oraristrix* among all owls examined (see list of genera above). Further, in addition to the osteological characters, many intra- and inter-element ratios set *Oraristrix* apart from *Bubo* and *Strix* (e.g., Figs 2, 3). These ratios give us a more complete picture of this owl, in comparison to *Strix* and *Bubo*, but they are informative rather than diagnostic characters. As with all other taxonomic categories, there is no fixed definition as to what comprises a genus, but in this case, we conclude

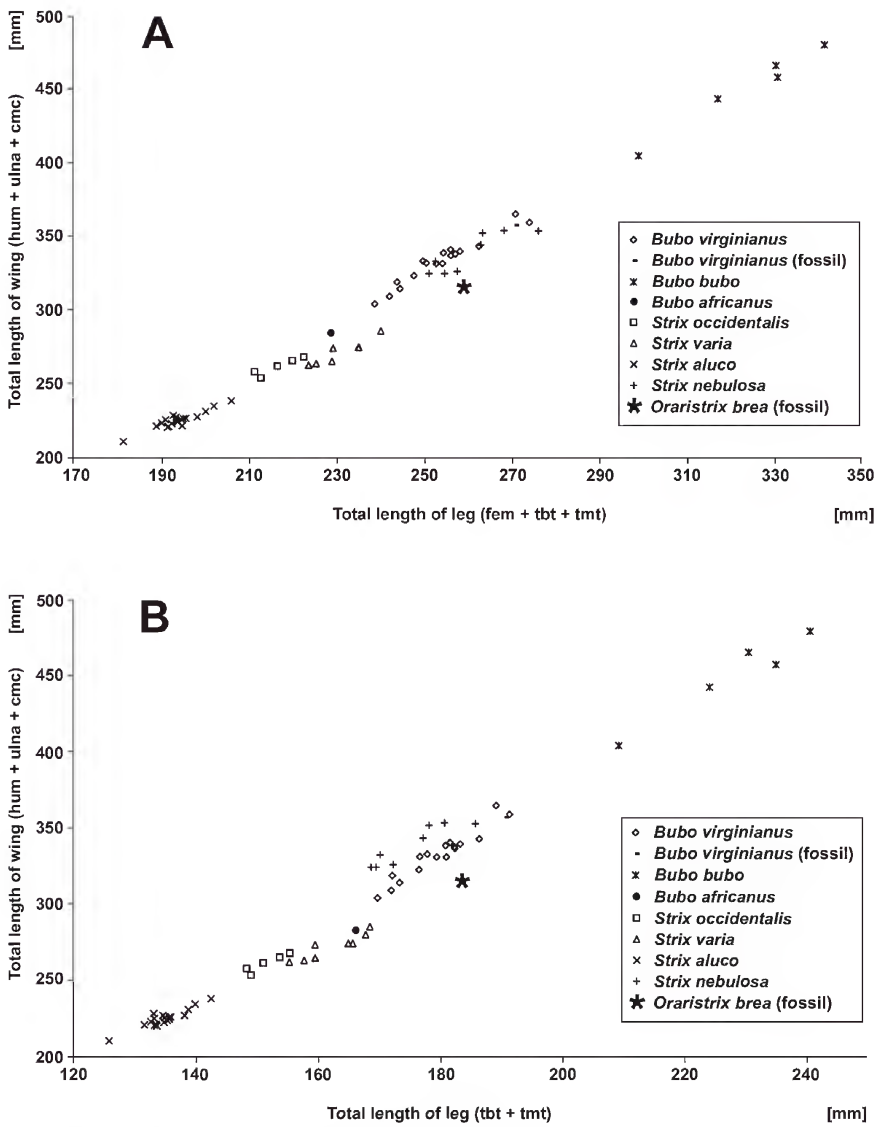


Figure 9. A comparison of wing length *vs.* leg lengths in *Bubo bubo, B. africanus, B. virginianus, Strix nebulosa, S. occidentalis, S. varia, S. aluco*, and *Oraristrix brea*. In (*A*) the leg length includes the femur, whereas in (*B*) only the tibiotarsus and the tarsometatarsus are included in the leg length because the femur is held in a near horizontal position and it correlates with the weight of the bird, not necessarily its stature. In both plots it can be seen that *O. brea* had relatively longer legs in comparison to species of similar wing length. However, the difference might also result from the small number of fossil specimens and/or the fact that the fossil *O. brea* is a composite of an unknown number of individuals. We cannot exclude the possibility, however remote, that the leg elements all, or primarily, belong to large females whereas the wing bones are all from smaller males.
For the modern species, each symbol represents one specimen, whereas for *Oraristrix brea* and the fossil *Bubo virginianus* from Rancho La Brea the symbol stands for the arithmetic means of all fossil specimens of particular elements. For *O. brea* the number of fossil specimens available for calculating the means was as follows: humerus, 4; ulna, 1; carpometacarpus, 7; femur, 5; tibiotarsus, 5; tarsometatarsus, 15. For fossil *B. virginianus*, the number of specimens available for calculating the means was as follows: humerus, 6; ulna, 6; carpometacarpus, 34; femur, 41; tibiotarsus, 18; tarsometatarsus, 68.

that the mosaic of distinctive osteological characters found for the Brea Owl is strong support for the recognition of a new genus.

Given the mosaic of characters, and the lack of complete skeletons (e.g., no skulls are known), it is not possible at the present time to say whether *Oraristrix* is derived from either *Bubo* or *Strix*, or an as yet unknown, extinct lineage. If, as the molecular evidence suggests (Wink & Heidrich, 1999; Wink *et al.*, 2008), *Strix* and *Bubo* are closely related, then the ancestral lineage of *Oraristrix* might remain unresolved for some time.

Distribution at Rancho La Brea. Howard (1962) reported 56 specimens of *Oraristrix brea*, representing a minimum of 17 individuals from seven pits at Rancho La Brea. The 138 specimens we have identified as *O. brea* from Rancho La Brea represent a minimum of 23 individuals from 13 pits (Table 2). Howard (1962) found that the greatest number of specimens of *O. brea* came from Pit 16, which she reported as having almost twice as many individuals of all species of birds preserved as the pit with the second-highest minimum number of individuals of all species of birds at Rancho La Brea. Similarly, we found 58 specimens from Pit 16, almost

Table 2. Distribution of *Oraristrix brea* among the different pits, or excavation sites, at Rancho La Brea, with a summary of minimum number of individuals per pit and in total. Scores given in the form left/right.

	Bliss 29	Pit A	Pit B	3	4	10	16	28	36	61–67	81	Pit 91	LACM 7247	total
Rostrum maxillare	·	·	·	·	1	·	·	·	1	·	·	·	·	2
Mandible	·	1/–	·	·	·	·	·	·	·	·	·	·	·	1
Sternum	·	·	·	1	·	·	2	·	·	·	·	·	·	3
Scapula	·	2/–	·	1/–	·	·	5/4	·	·	·	–/1	1/–	·	14
Furculum	·	·	·	1/–	·	·	·	·	·	·	·	·	·	1
Coracoid	·	·	·	1/–	·	·	2/5	·	·	1/–	·	·	·	9
Coracoid–Scapular end	–/1	2/–	·	·	·	·	·	·	·	·	·	·	·	3
Humerus	·	·	·	1/–	–/1	1/1	–/1	·	·	·	·	·	·	5
Humerus–Proximal	·	1/–	–/1	·	·	·	1/–	·	·	·	·	·	·	3
Humerus–Distal	·	·	·	1/1	·	·	1/–	·	·	·	·	·	·	3
Ulna	·	·	·	·	·	·	–/1	·	·	·	·	·	·	1
Ulna–Proximal	·	·	·	1/–	1/–	·	–/2	·	·	·	·	·	·	4
Ulna–Distal	·	1/1	·	·	·	·	–/1	–/1	·	·	·	·	·	4
Radius														
Radius–Proximal	·	2/–	·	1/–	·	·	1/–	·	·	·	·	·	1/–	5
Radius–Distal	·	1/1	·	·	·	·	1/–	·	·	·	·	·	·	3
Carpometacarpus	1/–	1/–	·	–/1	–/1	·	3/4	·	·	·	·	·	·	11
Carpometacarpus–Distal	·	2/–	·	·	·	·	·	·	·	·	·	·	·	2
Pelvis–Synsacra	·	·	·	·	1	·	1	·	·	·	·	·	·	2
Femur	·	–/1	·	·	1/–	·	2/1	·	·	·	·	·	·	5
Femur–Proximal	·	1/–	1/–	·	·	·	·	·	·	·	·	·	·	2
Femur–Distal	·	2/1	2/–	·	·	·	–/4	·	·	·	·	1/–	·	10
Tibiotarsus	·	·	·	1/–	1/1	·	1/–	·	·	–/1	·	·	·	5
Tibiotarsus–Proximal	·	–/1	1/–	·	1/–	·	3/–	·	·	·	·	·	·	6
Tibiotarsus–Distal	–/2	1/1	–/2	·	–/2	·	–/3	·	·	·	·	·	1/–	12
Fibula	·	1/–	·	·	·	·	1/–	·	1/–	·	·	·	·	3
Tarsometatarsus	1/–	3/3	·	·	2/–	·	4/4	·	·	·	·	·	·	17
Tarsometatarsus–Prox	·	·	·	·	·	·	·	·	·	·	·	·	–/1	1
Tarsometatarsus–Distal	·	1/–	·	·	·	·	·	·	·	·	·	·	·	1
total specimens	5	31	7	11	13	2	58	1	2	1	1	2	3	138
minimum individuals	2	3	2	1	2	1	5	1	1	1	1	1	1	23

twice as many as from Pit A, which produced 31 specimens. Six pits produced only one or two specimens. The presence of *O. brea* in the collections from Carpinteria, California, a coastal site approximately 130 km northwest of Rancho La Brea, suggests that *O. brea* was widespread in the coastal lowlands of southern California in the late Pleistocene.

Other records of *Oraristrix brea*. *Oraristrix brea*, as *Strix brea*, has been reported from four other localities outside of southwestern California. One tentative record was reported from Dry Cave, New Mexico (Hurley, 1972), but this record was later corrected because the specimen represents *Bubo virginianus* (A. Harris, pers. comm., see http://www.utep.edu/leb/pleistNM/). A second record, from Sangamon interglacial deposits at Rancho la Brisca, Sonora, Mexico, was reported by Van Devender *et al.* (1985). Examination of a cast of this specimen, a partial tarsometatarsus, housed at the University of Arizona Laboratory of Paleontology (UALP 10157), revealed that it was more similar to *Strix* than to *Bubo* in having a much shorter, proximodistally, Trochlea metatarsi III, which also had its lateral rim much shorter anteroposteriorly and relatively straight, not rounded, posteriorly. Although the available cast showed that the specimen was strongly abraded in some areas, it differed from *Oraristrix* in having (*a*) Trochlea metatarsi III not bulging laterad, in distal view; (*b*) Trochlea metatarsi III shorter, proximodistally, with long axis at a greater angle to long axis of shaft; (*c*) Trochlea metatarsi IV, in lateral view, more rounded distally; (*d*) Fac. lateralis where leading to Trochlea metatarsi IV much broader anteroposteriorly, in lateral view; (*e*) Fac. medialis flatter and broader anteroposteriorly at mid-shaft; and, although only partially visible, (*f*) Sulcus extensorius clearly not as deep along medial edge of Tuberositas m. tibialis anticus, and groove lateral to Tuberositas m. tibialis anticus more constrained, or narrower. Based on the above characters it must be concluded that the specimen does not represent the Brea Owl. Given the poor condition of the specimen, its true identity remains unknown.

A complete tarsometatarsus (Mesa Southwest Museum P6437) from the late Blancan 111 Ranch local fauna near Safford, southeastern Arizona has been referred to *Oraristrix brea* (D. Steadman, pers. comm.). Also, two additional specimens, a partial tarsometatarsus and an unidentified partial pedal phalanx from upper Pleistocene (Rancholabrean Land Mammal Age) fossil deposits at Térapa in east-central Sonora, Mexico, have been referred to *Oraristrix brea* (D. Steadman, pers. comm.). We were unable to examine these specimens, so we cannot comment on the accuracy of their identifications.

***Oraristrix*: an "island" owl?** In many ways, southwestern, coastal California currently comprises an island. It is bordered on the west by the Pacific Ocean and surrounded to the north, east, and south by high mountains and/or extreme deserts. For sedentary, or non-migratory, species of birds that somehow found their way into southwestern, coastal California there would probably have been little opportunity for interbreeding with ancestral lineages. Isolation would have led to allopatric speciation, although we cannot yet suggest a time of divergence for *Oraristrix* from its ancestral lineage. However, the many osteological differences between *Oraristrix*, on the one hand, and *Bubo* and *Strix* on the other, suggest to us that the time of divergence of *Oraristrix* was well before the late Pleistocene. If the record from the 111 Ranch local fauna is accurate, the species' ancestral lineage might have entered southern California in the latest Pliocene or earliest Pleistocene.

The island analogy is perhaps supported by the allomorphic direction *Oraristrix* took relative to *Strix* and *Bubo*. Specifically, the increase in leg length, and especially of the length of the tarsometatarsus, relative to wing length and the very large premaxillary can be interpreted as features derived from an island lifestyle. As Louchart (2005:170) noted, in island owls "Trends for longer hindlimbs and shorter wings are observed, and are the same as those known in island birds in general. The most general explanations lie in terrestriality, special diets, and sedentarity." This observation follows that of Grant (1965a:364) in which "In North America and Mexico there is a strong tendency for island birds to have a longer tarsus and bill than their mainland counterparts; ..." and "The bill is longer because it deals with a greater range of food-sizes, and the tarsus is longer because a greater variety of perches is used." Additional thoughts bearing on this subject are found in Grant (1965b, 1966). Although the wing:leg ratio in *Oraristrix* did not change as dramatically as that seen in the Hawaiian *Grallistrix*, it is still distinctly different from that seen in North American *Strix* and *Bubo*.

In addition to the species of *Grallistrix*, another example of congeneric island owls having lengthened hindlimbs and shortened wings is that of the genus *Mascarenotus* Mourer-Chauviré, Bour, Moutou, & Ribes, 1994 of the Mascarene Islands. Other island owl taxa were reviewed by Louchart (2005).

A final corollary with island owls is the timing of their extinction. As noted by Louchart (2005:170), "For the Strigiformes, even if the exact causes [of extinction] are often very difficult to establish, it was demonstrated in almost all the individual cases that they [reasons for extinction] were anthropogenetic." Although a clear link between the arrival of humans in southern California and the extinction of *Oraristrix brea* cannot be drawn, as opposed to the more obvious possible link noted for the extinction of the California Turkey, *Meleagris californica* (Bocheński & Campbell, 2006), the two events did seem to occur at approximately the same time.

Conclusion

A review of the large, extinct owl from Rancho La Brea has more than doubled the number of specimens and added new skeletal elements to those previously known for that species. A larger series of modern comparative material than that available in 1933, when the species was first described, as well as many more specimens of the extinct species, facilitated the identification and description of more osteological features of *Oraristrix brea*. In some instances, osteological characters could be correlated between articulating bones, thereby placing them into a larger context. The many distinctive characters of the bones comprising the knee joint, for example, suggest that pedal locomotion and/or prey capture was probably different in *Oraristrix* when compared to that of *Strix* and *Bubo*. The estimated weight of *O. brea* is consistent with the interpretation that it was a slender-bodied bird, and its longer legs relative to its wingspan when compared with *Bubo* or *Strix*, as well as many inter- and intra-membranal ratios, set the extinct Brea Owl apart as a long-legged owl. We interpret these features as suggesting that this owl was more terrestrial in habits, favoring coastal scrub habitats, as opposed to being a forest owl. We conclude that the distinctive osteological features of this owl warrant its placement in a new genus, *Oraristrix*.

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Appendix 1

List of catalogue numbers of specimens of *Oraristrix brea* (* indicates photograph of specimen appears in a figure; *H indicates holotype).

Rancho La Brea

All catalogue numbers of Rancho La Brea specimens carry the prefix "LACM RLB."

Rostrum maxillare	C7125, K2713*
Mandible	K9915
Sternum	F2477*, F2530, D9615
Scapula	
Right	H6610, H6629, H6659, H6660, H6673
Left	E2720, H6039, H6065, H6613*, H6636, H6656, K9439, K9440, R11681
Coracoid	
Right	E9687*, H4850, H4889, H4904, H4911
Scapular end	K9435
Left	E9273, H4872, H4881, H4923
Scapular end	K9436, K9437
Clavicula	E9233*
Humerus	
Right	E9425, E9804*, F9702
Proximal	K5261
Distal	E8911
Left	F9701, E9051
Proximal	F9305, K9438
Distal	G2129, F9538
Ulna	
Right	E9544*
Proximal	F1293, G8424
Distal	G8426, K9750
Left	
Proximal	D296, E3170
Distal	G8435, K9753
Radius	
Right	
Distal	K9629
Left	
Proximal	E9025, H8036, K9797, K9798*, L481
Distal	H8026, K9627*
Carpometacarpus	
Left	E1155, H3107, H3126, K9432*
Right	E3820, E4504, H3096, H3097, H3098, H3124, K9434
Distal	K9431, K9433
Pelvis	F1325, F3700
Femur	
Right	E9647, K9427*
Distal	F4880, F4883, F4884, F6043, K9424
Left	B9889, E9439, E9909
Proximal	K9370, K9428*
Distal	K9425, K9426, K9429, K9430, R45378
Tibiotarsus	
Right	E9758, E9932
Proximal	K9505
Distal	E1139, E9363, E9919, E9942, F7456, K5259, K9506, K9512, K9513
Left	E9267, E9414, E9888*
Proximal	E680, E4347, E9545, E9606, K5260
Distal	K9503, K9511, R49134
Fibula	
Left	K1040, H9244*, L483
Tarsometatarsus	
Right	E9416, E9575, G3933, G3958, K9620, K9621, K9622, K9623*
Proximal	L482
Left	E9379*H, E9417, E9892, E9911, G3931, G3957, K9616, K9617, K9619
Distal	K9618

Carpinteria Locality LACM(CIT) 139

Rostrum maxillare	LACM 154059
Coracoid	
Right	LACM 154054
Left	LACM 154055
Humerus	
Left	LACM 154058
Proximal	LACM 154060
Carpometacarpus	
Left	LACM 154056
Tarsometatarsus	
Left	LACM 154051

Santa Barbara Museum of Natural History

Coracoid	
Right, sternal end	SBMNH 1243
Tibiotarsus	
Right, distal	SBMNH 773

Appendix 2

Illustrations of measurements taken (Figs 10–11).

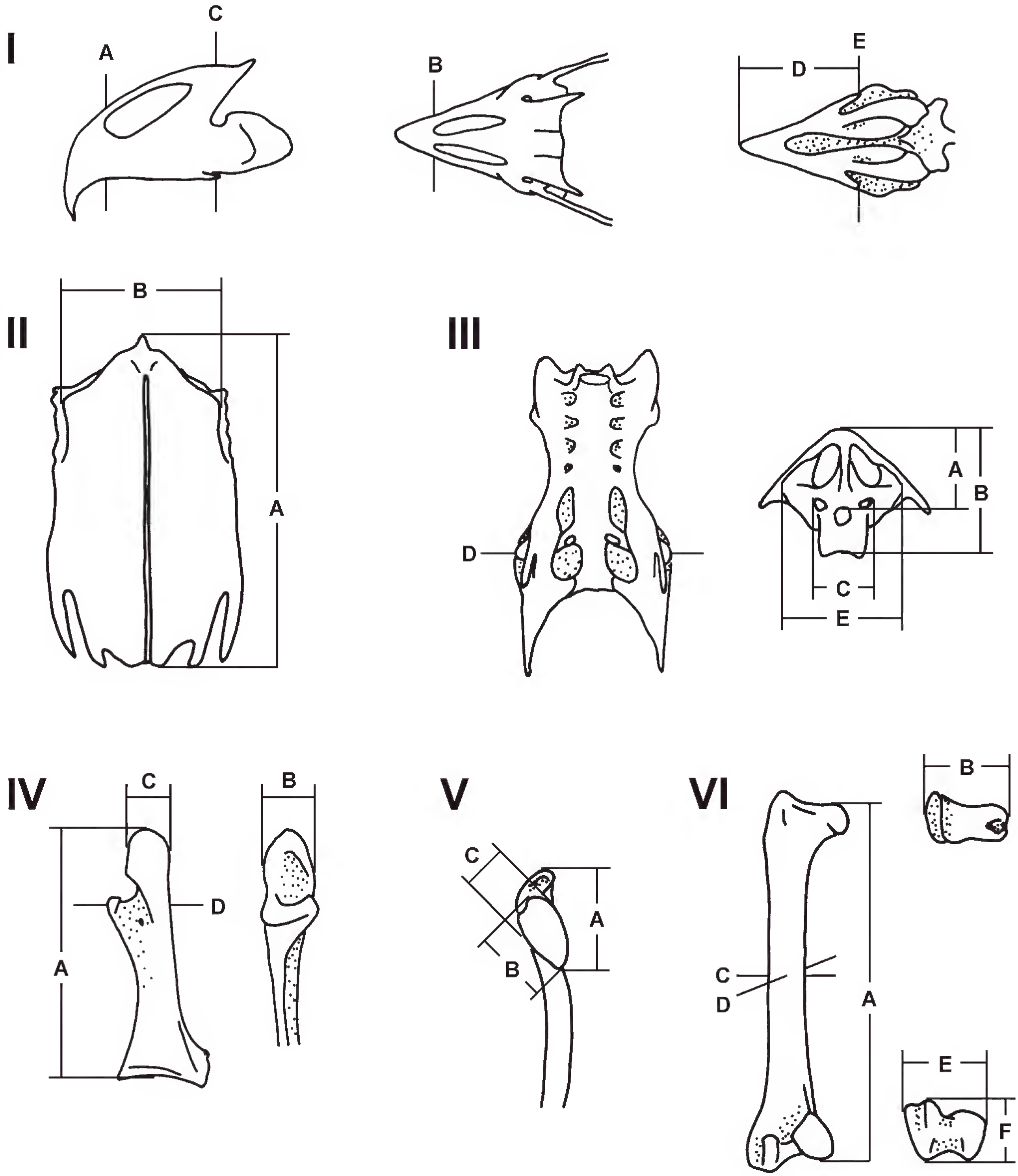

Figure 10. Measurements (refer to Table 1). (*I*) Premaxilla: A, anterior height; B, anterior width; C, posterior height; D, tomial length; E, tomial width. (*II*) Sternum: A, total length; B, ventral width. (*III*) Pelvis: A, neural arch height; B, centre height through vertebra; C, width through prezygapophyses; D, width through antitrochanter; E, width through 1st transverse process. (*IV*) Coracoid: A, length to mid-Fac. artic. sternalis; B, depth of acrocoracoid; C, width of acrocoracoid; D, width of shaft at procoracoid. (*V*) Scapula: A, articular length; B, length of Fac. artic. humeralis; C, width of Fac. artic. humeralis. (*VI*) Femur: A, median length; B, proximal width; C, width at midshaft; D, depth at midshaft; E, distal width; F, distal depth.

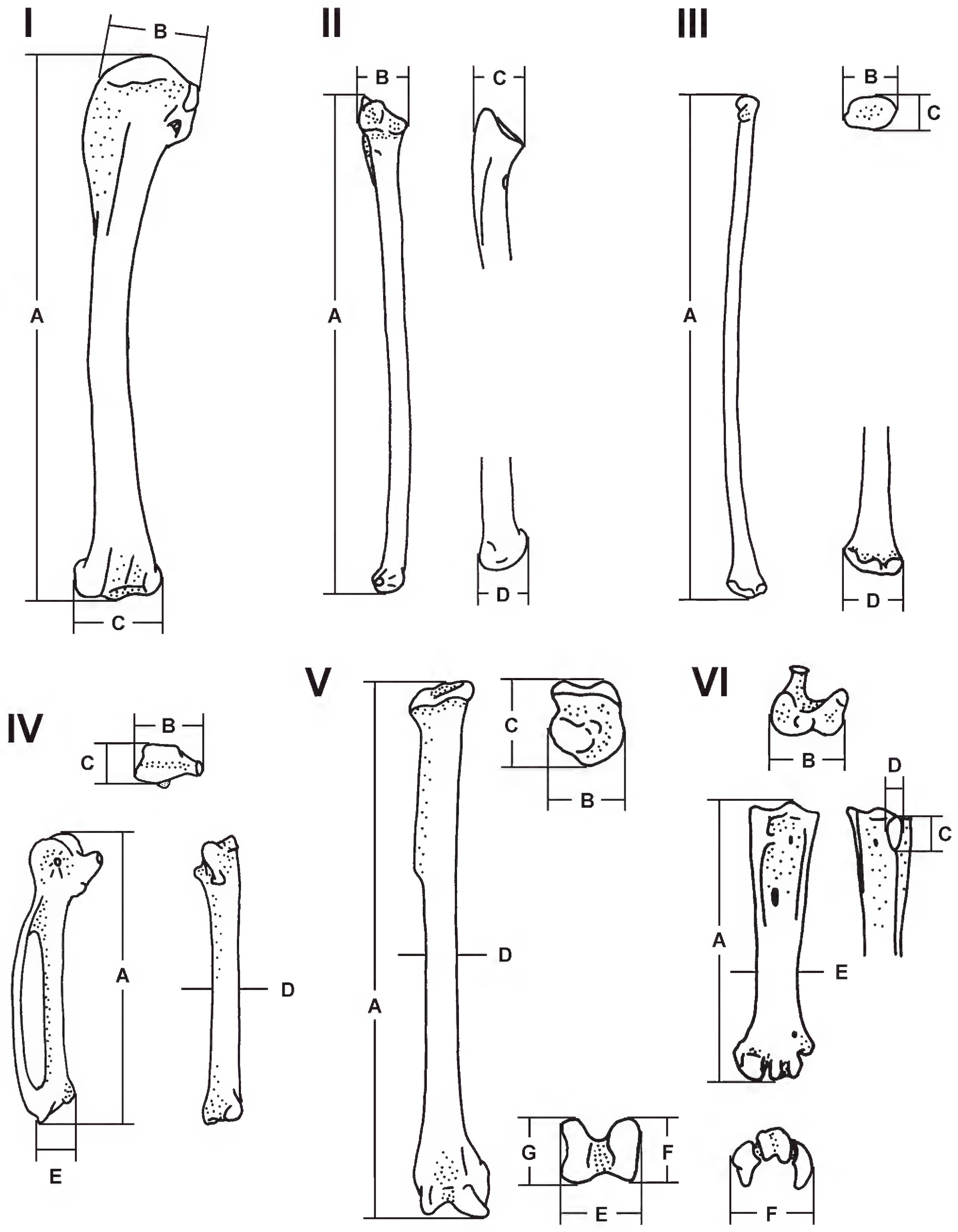

Figure 11. Measurements (refer to Table 1). (*I*) Humerus: A, total length; B, proximal width; C, distal width. (*II*) Ulna: A, total length; B, proximal width; C, proximal depth; D, width of Condylus dorsalis. (*III*) Radius: A, total length; B, maximum proximal width; C, minimum proximal width; D, distal width. (*IV*) Carpometacarpus: A, total length; B, proximal width; C, proximal depth; D, depth of mid shaft; E, distal width. (*V*) Tibiotarsus: A, total length; B, proximal width; C, proximal depth; D, width at midshaft; E, distal width; F, depth of Condylus lateralis; G, depth of Condylus medialis. (*VI*) Tarsometatarsus: A, total length; B, proximal width; C, length of hypotarsus; D, width of hypotarsus; E, minimum shaft width; F, distal width.